Beluga \textit{(Delphinapterus leucas)} Adult Life Expectancy: Wild Populations vs the Population in Human Care

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Life expectancy is a commonly used measure of the overall health and quality of life among human populations and within a human population over time (\textit{e.g.}, the Center for Disease Control [2010], the World Health Organization [2011], and the Central Intelligence Agency [2011]). This measure can also be used for comparing the relative health and quality of life of populations of non-human animal species. The objective of this study is to use published values of life expectancy for beluga in the wild and beluga in human care to compare the relative health and quality of life of beluga in these two environments. There are two commonly used measures of life expectancy: the median and the average. The median life expectancy is the age to which 50\% of individuals are expected to live. Thus, the median is the life expectancy of the typical individual. The average life expectancy is an estimate of how long individuals are expected to live on average. In most cases the average is greater than the median as it is more influenced by individuals that live very long lives.

\textbf{Adult Life Expectancy of Wild Beluga}

Determining the life expectancy of wild beluga is complicated by two factors. First, there are two hypotheses regarding the rate of deposition of tooth dentinal growth layer groups (GLGs). For many years, it was believed that two GLGs were deposited each year. Thus, the age of a wild beluga could be determined by removing a tooth, counting the number of GLGs, and dividing that number by two. This belief was based on a number of pieces of evidence including a comparison of teeth extracted from animals at the time of collection with other teeth
extracted a number of years later [Sergeant 1973]. In later studies teeth were marked by treating beluga with tetracycline. Years later a tooth was removed and the GLGs formed subsequent to the treatment were counted [Brodie et al. 1990].

Stewart et al. [2006] concluded that only a single GLG was formed each year based on the radioactive signature of atomic bombs detonated in the late 1950s and early 1960s found in tooth GLGs of wild beluga. Although this result seems definitive, it does not directly refute the findings of earlier studies and does not address a possible difference in rates of GLG deposition in early age classes. A workshop held specifically to address this issue was unable to definitively conclude that the one GLG/year model was correct. Lockyer et al. [2007] stated that at the workshop “... it was not possible to reach consensus in the identification of GLGs or their deposition rates ...” but that “the results from this study clearly indicated that an annual deposition rate was most likely.” Because the annual deposition rate is the more likely it will be assumed that it is correct in the calculations below. The implication is that the estimate based on one GLG/year should be considered the likely maximum age. That is, if it is later determined that multiple GLGs are deposited in some years then the estimates of adult life expectancy calculated below will be overestimates.

The second complicating factor for determining the life expectancy of wild beluga is that nearly all studies on the demography of wild beluga are based on estimated ages of beluga that were harvested. This creates a bias towards larger animals because typically only larger animals are harvested. This means animals in the first few age classes are under sampled or are entirely absent from the sample. The standard method for dealing with this bias is to assume that from a given starting age (usually one year) the probability of death is a constant. That is, the probability that a one year old beluga survives to its next birthday is the same as the probability
that a 40 year old beluga survives to its next birthday. Thus, a single Annual Survival Rate (ASR) describes the survivorship of all animals over one year of age regardless of their age [DeMaster and Drevenak 1988].

Using the conclusion that one GLG/year is the more likely model alters the interpretation of demographic data in all studies of beluga published prior to 2006. The values reported in those publications must be updated to conform to the one GLG/year model. An ASR reported under the two GLGs/year model is actually an estimate of two year survival assuming the one GLG/year model is correct. Converting a two year survival rate into a one year survival rate (ASR) is accomplished by taking the square root of the reported value. The median adult life expectancy of an animal from a year of age can be calculated directly from the ASR value as $\ln(0.50)/\ln(\text{ASR})$, and the average adult life expectancy is calculated as $-1/\ln(\text{ASR})$ [Seber, 1973].

Hobbs and Sheldon [2008] reviewed the literature on wild beluga demography and presented the ASR findings from five studies in their Table 2.3.3-1. Those reported values are presented in Table 1 below, along with a correction for a one GLG/year model and the corresponding median and average adult life expectancy.

Table 1: Adult Life Expectancy adjusted for a 1 GLG/year model from studies cited in Hobbs and Sheldon [2008].

<table>
<thead>
<tr>
<th>Study</th>
<th>Reported ASR</th>
<th>ASR for 1 GLG/year</th>
<th>Median Adult Life Expectancy</th>
<th>Average Adult Life Expectancy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oshumi, 1979</td>
<td>0.842</td>
<td>0.9176</td>
<td>8.06</td>
<td>11.63</td>
</tr>
<tr>
<td>Oshumi, 1979</td>
<td>0.905</td>
<td>0.9513</td>
<td>13.89</td>
<td>20.03</td>
</tr>
<tr>
<td>Braham, 1984</td>
<td>0.91</td>
<td>0.9539</td>
<td>14.70</td>
<td>21.19</td>
</tr>
<tr>
<td>Braham, 1984</td>
<td>0.92</td>
<td>0.9592</td>
<td>16.63</td>
<td>24.01</td>
</tr>
<tr>
<td>Burns and Seaman, 1986</td>
<td>0.9064</td>
<td>0.9521</td>
<td>14.11</td>
<td>20.37</td>
</tr>
<tr>
<td>Study</td>
<td>Reported ASR</td>
<td>ASR for 1 GLG/year</td>
<td>Median Adult Life Expectancy</td>
<td>Average Adult Life Expectancy</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>--------------</td>
<td>--------------------</td>
<td>-----------------------------</td>
<td>------------------------------</td>
</tr>
<tr>
<td>Beland, et al., 1992</td>
<td>0.96</td>
<td>0.9798</td>
<td>33.96</td>
<td>49.00</td>
</tr>
<tr>
<td>Beland, et al., 1992</td>
<td>0.97</td>
<td>0.9849</td>
<td>45.51</td>
<td>65.72</td>
</tr>
<tr>
<td>Lessage and Kingsley, 1998</td>
<td>0.935</td>
<td>0.9670</td>
<td>20.63</td>
<td>29.80</td>
</tr>
</tbody>
</table>

As seen in Table 1, there is large range in the estimates of median and average adult life expectancy reported in these studies. The reason is likely due to several factors including differences among the studied populations, sampling methodology (harvested versus stranded beluga), and the statistical methodologies used to derive the estimates. As an example of the latter, Burns and Seaman [1986] provided both an estimate of “mean annual mortality” as well as a life table. The life table approach yielded a value 50% larger than the value obtained by applying the ASR method to the same data. Beland et al. [1988, and reported again in Beland et al. 1992] based their estimate of ASR on the life table developed by Burns and Seaman [1986]. The life table approach to calculate an ASR likely led to values reported by Beland et al. [1988] and Beland et al. [1992] that appear well outside of the range of the other studies.

It should be noted that the review by Hobbs and Sheldon [2008] was not exhaustive. There are a number of more recent studies on the demography of wild beluga populations in which ASR is reported. For example, Heide-Jorgensen and Lockyer [2001] report ASR values for male and female beluga from populations in West Greenland and western Russia. Once adjusted for one GLG/year and converted into adult life expectancy, their estimates of the median age range from 4.4 to 10.8 years and estimates of the average age range from 6.3 to 15.6 years. This particular study is cited as it suggests that some of the variation in estimates of median life expectancy among studies (as seen in Table 1) may arise from natural variation among studied populations and between the sexes.
There is no single definitive answer to the question “What is the adult life expectancy of beluga in the wild?” It does not make sense to simply take an average of the values reported by Hobbs and Sheldon [2008] because the selection of studies could have a greater bearing on the outcome than the variable of interest (the general health and quality of life of wild beluga). Omitting the studies that reported the lowest [Oshumi 1979] and highest [Beland et al. 1992] values in Table 1 as being probably non-representative suggests that most wild populations would have a median adult life expectancy of somewhere between 15 and 21 years, and an average life expectancy of between 21 and 30 years. Note that the median and average values reported in Table 1 differ considerably. This difference is likely in part an artifact of the assumption that annual survival rates are constants. If the probability of survival decreases with advanced age in beluga populations (as it does in human populations), then the average based on the ASR method will be an overestimate.\(^1\) On the other hand, the median would be largely unaffected. Therefore, the estimate of median life expectancy is likely to be the more accurate measure.

**Adult Life Expectancy of Beluga in Human Care**

Even though life tables are frequently used for demographic analysis of populations of animals in human care, to be directly comparable to estimates for wild beluga the ASR methodology must also be used for the population of beluga in human care. Estimation of life expectancy of beluga in human care is more straightforward than is the case for wild beluga. The complication of biased sampling resulting from harvesting beluga is not a factor, nor is the issue of one versus two tooth GLGs/year. The ASR method for animals under constant

\(^1\) When calculating life expectancy from the Annual Survival Rate there is theoretically no maximum age limit. Although the calculated probability of a beluga living to, for example, 100 or more years is extremely small, it does add to the average life expectancy. In calculating a median the magnitude of the individual lifespans are not used. Therefore, the median life expectancy is not influenced by these only theoretically possible (i.e., never observed) life spans.
observation requires no estimate of the age of animals. All that is needed is the number of years each animal over the age of one year lived in human care and whether or not the animal is still alive.

Data on the population of beluga in human care in the United States are available in the National Marine Fisheries Service (NMFS) Marine Mammal Inventory Report (MMIR). These data have been used by many researchers to estimate the life expectancies of several marine mammal species. Table 2 contains the results of four studies on life expectancy of beluga in human care.

Table 2: Estimates of adult life expectancy obtained from analysis of data in the NMFS MMIR.

<table>
<thead>
<tr>
<th>Study</th>
<th>Time Period</th>
<th>Reported ASR</th>
<th>Median Life Expectancy</th>
<th>Average Life Expectancy</th>
</tr>
</thead>
<tbody>
<tr>
<td>DeMaster and Drevenak, 1988</td>
<td>1973-1985</td>
<td>0.94</td>
<td>11.20</td>
<td>16.16</td>
</tr>
<tr>
<td>Woodley et. al, 1997</td>
<td>1973-1994</td>
<td>0.946</td>
<td>12.48</td>
<td>18.01</td>
</tr>
<tr>
<td>Innes et. al, 2005</td>
<td>1973-2003</td>
<td>0.97</td>
<td>22.76</td>
<td>32.83</td>
</tr>
</tbody>
</table>

**Conclusion**

There is very high variation in the estimates of life expectancy among studies of wild beluga populations for numerous reasons. Therefore, presenting a single estimate as being representative is not reasonable. The median life expectancy in wild beluga populations is likely between 15 and 21 years and the average life expectancy is likely between 21 and 30 years. Because all studies of beluga in human care are based on the NMFS MMIR, the estimates among studies are much more consistent. The range of values from those studies is almost identical to those reported for wild beluga. The range in median life expectancy for belugas in human care is
from 11 to 23 years and the range for average life expectancy is 18 to 33 years. There is in fact complete overlap in these ranges. Therefore, based on life expectancy as a measure of the general health and the quality of life in a population, wild beluga and beluga in human care are effectively identical.
Literature Cited


