HARBOR PORPOISE AND FISHERIES: AN UNCERTAINTY ANALYSIS OF INCIDENTAL MORTALITY

HAL CASWELL,1 SOLANGE BRAULT,2 ANDREW J. READ,3 AND TIM D. SMITH4

1Biology Department, MS 34, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543 USA
2Biology Department, University of Massachusetts, 100 Morrissey Boulevard, Boston, Massachusetts 02125 USA
3Duke University Marine Laboratory, Beaufort, North Carolina 28516-9721 USA
4Northeast Fisheries Science Center, National Marine Fisheries Service, Woods Hole, Massachusetts 02543 USA

Abstract. The harbor porpoise (Phocoena phocoena) in the western North Atlantic is subject to mortality due to entanglement in gillnets. Such incidental mortality threatens a population if it is too large relative to the potential population growth rate. Critical values for incidental mortality have been established by the International Whaling Commission and the U.S. Marine Mammal Protection Act. As in many situations in conservation biology, use of these critical values depends on demographic calculations that are based on uncertain data. It is important to report not only estimates of demographic parameters, but also the uncertainty in those estimates. Here, we use a Monte Carlo approach to evaluate uncertainty in population size, incidental mortality, and population growth rate of harbor porpoise. To describe survival, we used model life tables derived from other mammals with similar life histories. By randomly sampling the space of model life tables and the distributions of estimated fertility and age at first reproduction, we produced a probability distribution that characterizes the uncertainty in the potential population growth rate. The median estimate for the potential annual rate of increase $\lambda$ is approximately 1.10. Combining this information with the uncertainty of incidental mortality and of population size, we estimate the probability that the rate of incidental mortality exceeds the critical values established by the various management agencies; this probability ranges from 0.46 to 0.94. We conclude that recent incidental mortality rates are a threat to harbor porpoise populations. The methods developed here are applicable to other situations in which demographic analyses must be based on uncertain data.

Key words: conservation biology; harbor porpoise; incidental mortality; Marine Mammal Protection Act; matrix population models; Monte Carlo methods; Phocoena phocoena; population growth rate; uncertainty analysis.

INTRODUCTION

Conservation biologists often need estimates of demographic statistics for endangered or threatened species, in order to provide advice to managers and policy makers. Such statistics include population size, mortality rates, rates of increase, sensitivities and elasticities of rates of increase, and extinction probabilities (e.g., Crouse et al. 1987, Dennis et al. 1991, Crowder et al. 1994, Doak et al. 1994, Heppell et al. 1994, Fiedler and Kareiva 1998). They must be computed from data that are always uncertain, sometimes extremely so. This uncertainty in the demographic data translates into uncertainty in the estimates of population statistics. However, because of the complex calculations involved in transforming the basic data into demographic statistics, it can be difficult to estimate that uncertainty. In some cases, the data must be supplemented with estimates extrapolated from other species or drawn from the literature or expert opinion, making it even more difficult to quantify the uncertainty.

The situation of the harbor porpoise (Phocoena phocoena) in the western North Atlantic is such a case. The harbor porpoise is a small (45–70 kg) cetacean, found in shallow, coastal waters of the temperate to subarctic Northern Hemisphere. In the western North Atlantic, it occurs from Labrador south to North Carolina. It is listed as a threatened species in Canada, and a petition was filed in 1993 to list it as threatened under the U.S. Endangered Species Act (Federal Register 58: 3108–3120). The Gulf of Maine and Bay of Fundy stock has been classified as "strategic" by the National Marine Fisheries Service, under the provisions of the Marine Mammal Protection Act (Blaylock et al. 1995, Waring et al. 1997).

Harbor porpoise are subject to incidental mortality from entanglement in sink gillnets. Whether or not this incidental mortality is a threat to the population depends on its magnitude relative to the potential rate of increase (i.e., the population growth rate at low densities). Incidental mortality that exceeds the potential rate of increase will, in the long run, drive a population to extinction. Prudence suggests that incidental mortality should be kept below some critical value, which is less than the potential rate of increase. Both the
International Whaling Commission (IWC) and the Marine Mammal Protection Act have established such critical values. In the case of the Marine Mammal Protection Act, incidental mortality in excess of the critical value has immediate management consequences.

Determining whether incidental mortality exceeds a specific critical value requires estimates of three quantities: population size, the number of animals taken as by-catch, and the potential rate of increase of the population. Each of these quantities is known only with uncertainty, and our goal is to assess how this uncertainty affects the final conclusions. In doing so, we will go considerably beyond the provisions of the Marine Mammal Protection Act, which does not consider the uncertainty in these quantities.

**Approaches to measuring uncertainty**

Uncertainty and its measurement are important to scientists, managers, and policy makers. Attempts to legislate the reporting of uncertainty in risk assessments are increasingly frequent (Davies 1995). For an example from the United States, see the Department of Energy Risk Management Act of 1995 (S. 333), which would have required the inclusion of “an array of multiple estimates (showing the distribution of estimates and the best estimate) based on assumptions, inferences, or models which are equally plausible, given current scientific understanding” in any risk assessment document.

It is an obvious mistake to ignore the uncertainty of an estimate, especially if that estimate has management implications. It is equally a mistake to use the mere existence of uncertainty as an excuse to avoid management action (for examples from the history of marine fisheries, see Smith 1994). To avoid such mistakes, it is important to quantify and document the uncertainty, and to take it into account in making policy.

Approaches to estimating uncertainty fall, more or less, into three categories. First, there are the statistically easy cases. If the quantity being calculated is simple enough and is based on samples from a known distribution, then classical statistical theory provides methods for computing standard errors and confidence intervals. Second, there are cases in which standard errors and confidence intervals can be computed by bootstrap resampling methods (Efron and Tibshirani 1993). These require no assumptions about sampling distributions, but do require that the statistic be based on a sample of some well-defined units that can be resampled to generate the bootstrap distribution.

The harbor porpoise problem falls in a third category. Even the bootstrap does not apply, because the data are fragmentary, from different sources and of different types, or are not obtained from well-defined samples at all. Such problems can be attacked using Monte Carlo methods, if the investigator can specify statistical distributions that characterize the uncertainty in each of the parameters of the problem.

The essence of this approach is as follows. Suppose that $X$ is a random variable with a probability distribution $P_X(x)$, and that we are interested in another random variable $Y = f(X)$, which is a function of $X$. What is the distribution $P_Y(y)$ characterizing the uncertainty in $Y$?

If the distribution $P_X$ and the function $f(X)$ are simple enough, the distribution $P_Y$ may be calculated directly (e.g., any linear transformation of a normal random variable is also normally distributed). The Monte Carlo approach, which is independent of the complexity of $P_X$ or $f(X)$, begins by randomly generating many values of $X$, by sampling from $P_X$. The corresponding values of $Y$ are calculated. The empirical distribution of these values will, with probability one, converge to the true distribution of $P_Y$ as the number of samples becomes large. Alternatively, if $X$ takes only a few discrete values, sampling is not necessary, and a probability tree can be constructed showing the result of each possible value (e.g., Maguire et al. 1987).

In the present context, the random variable $X$ is an estimate of some quantity (e.g., population growth rate). Its probability distribution reflects the uncertainty in the estimate. Given lots of high-quality data, $P_X$ will be concentrated at one value of $X$. If the data are scarce or of poor quality, $P_X$ will have a much broader distribution. The Monte Carlo procedure shows how this uncertainty is transmitted to the estimate of $Y$. For general discussions of uncertainty analysis, see Cox and Baybutt (1981) and Morgan and Henrion (1988); Hertz (1964) is a particularly early description. Although Monte Carlo uncertainty analysis has been applied to ecosystem models (Gardner et al. 1981, O’Neill et al. 1982, 1983, Suter 1993), it has only occasionally been used in demographic calculations (e.g., Goodman 1984, Barnthouse et al. 1990, Ragen 1995, Powell et al. 1996).

In this paper, we will use Monte Carlo methods to calculate uncertainty in the potential population growth rate for harbor porpoise, and to compare the rate of incidental mortality to the critical values specified by different management bodies, in a manner that accounts for the aggregate uncertainty.

**The Harbor Porpoise Problem**

**By-catch and incidental mortality**

Harbor porpoises in the Gulf of Maine and Bay of Fundy are believed to form a relatively discrete population unit that can be managed as a separate stock (Blaylock et al. 1995, Waring et al. 1997). Estimates of the number of harbor porpoises taken annually as by-catch in the U.S. sink gillnet fishery in the Gulf of Maine between 1990 and 1993 range from 1200 to 2900 porpoises/yr (Bravington and Bisack 1996; see Table 1). Trippel et al. (1996) estimate that 424 and 101 harbor porpoises were taken as by-catch in the Bay of Fundy in Canada, in 1993 and 1994, respectively.
To transform these estimates of by-catch into incidental mortality rates, they must be divided by an estimate of population size. Sighting surveys using line transect methodology, conducted by the National Marine Fisheries Service in the summer of 1991 and 1992, yield an estimated total population size of 47 200 porpoises for the Gulf of Maine and Bay of Fundy (95% bootstrap confidence interval 32 500–70 600 porpoises; Smith et al. 1993, Palka 1995).

<table>
<thead>
<tr>
<th>Year</th>
<th>By-catch</th>
<th>Confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td>2900</td>
<td>1500–5500</td>
</tr>
<tr>
<td>1991</td>
<td>2000</td>
<td>1000–3800</td>
</tr>
<tr>
<td>1992</td>
<td>1200</td>
<td>800–1700</td>
</tr>
<tr>
<td>1993</td>
<td>1400</td>
<td>1000–2000</td>
</tr>
</tbody>
</table>

Policy implications of incidental mortality: how much is too much?

Dividing a total by-catch of about 2300 by a population size of about 47 200 yields an incidental mortality rate of approximately 5% per year. Is this cause for concern? It would be, of course, if it exceeded the potential rate of increase; this would eventually drive the population extinct. To be on the cautious side, however, incidental mortality should be maintained below some critical value strictly less than the potential rate of increase. In 1991, the Scientific Committee of the International Whaling Commission recommended that incidental mortality should not exceed half of the potential rate of increase (IWC 1991). In 1995, it added a recommendation that harvest and incidental mortality greater than one-fourth of the potential rate of increase should be considered cause for concern (IWC 1996).

Management of marine mammals in the United States (under the 1994 amendments to the Marine Mammal Protection Act) is based on the calculation of a “Potential Biological Removal.” The Potential Biological Removal is the maximum number of animals that can be removed from a population while still allowing it to remain at, or recover to, its “Optimum Sustainable Population” size, which ranges from the largest supportable population down to the population size maximizing net productivity (Barlow et al. 1995, Wade 1998). The Potential Biological Removal is the product of three quantities: one-half of the potential rate of increase, a minimum estimate of population size, and a “recovery factor” that ranges from 0.1 to 1.0. The minimum population size is defined as the 20th percentile of its sampling distribution, assumed to be lognormal. It is calculated as a function of the best estimate and its coefficient of variation (Wade 1998). The recovery factor reflects that status of the stock and the perceived quality of the data. A recovery factor of 0.1 is used for stocks classified as endangered or threatened under the Endangered Species Act. For other stocks, the recovery factor reflects uncertainty; the more uncertain the information about the stock, the smaller the recovery factor.

If the number of animals killed exceeds the Potential Biological Removal, the stock is classified as “strategic.” This classification has immediate management consequences; the Secretary of Commerce is required by law to prepare a take reduction plan, which will, within 6 mo of its implementation, reduce incidental mortality to a level judged to be compatible with recovery of the population. The plan must reduce mortality within 5 yr to “insignificant levels approaching zero mortality.”

The Potential Biological Removal represents a removal from the population that is considered safe from a management perspective. If it is converted to a mortality rate by dividing by the population size, the Marine Mammal Protection Act requirements can be rephrased: the incidental mortality rate must not exceed the product of one-half the rate of increase, the recovery factor, and the ratio of the 20th percentile of the population size distribution to the population size estimate. In the first stock assessment conducted under the amended Marine Mammal Protection Act, Blaylock et al. (1995) set the recovery factor for the harbor porpoise at 0.5 and the 20th percentile of the population size distribution at 0.854 of the estimated population. Thus, the critical mortality rate under that implementation of the Marine Mammal Protection Act (MMPA) is 0.2134 times the potential rate of increase. (A second stock assessment has recently been reported [Waring et al. 1997] in which the minimum population size is 0.89 of the best estimate. The recovery factor is unchanged at 0.5; this leads to a critical mortality rate of 0.22R, and would not noticeably change our conclusions.)

Thus, there exists a sequence of critical values for the incidental mortality rate. Let λ be the annual rate of increase, and define \( R = \lambda - 1 \) as the amount by which the population increases each year. Then the various critical values are:

- Maximum possible without extinction \( R \)
- IWC 1991 \( 0.5R \)
- IWC 1995 \( 0.25R \)
- MMPA \( 0.213R \).

In the next section, we estimate the potential rate of increase for the harbor porpoise, and, more important, the uncertainty of that estimate. We then combine that with the uncertainty in the estimates of by-catch and of population size to compute the probability that incidental mortality exceeds the critical values set by the various management agencies.
The age at first reproduction (AFR) is an important quantity in our calculations, because we use it to adjust the time scale of the life cycles of other species to match that of the harbor porpoise. There are several ways of estimating age at first reproduction (DeMaster 1984). Of these, we chose to estimate age at sexual maturity as the age at which 50% of the population has matured, and AFR as the age at sexual maturity plus an approximate gestation period.

We estimated age at sexual maturity by fitting a logistic regression to the proportion \( p(x) \) of individuals mature at age \( x \):

\[
\frac{p(x)}{1-p(x)} = \exp(b_1 + b_2x).
\]

We estimated \( b_1 \) and \( b_2 \) by weighted least squares (Chatterjee and Price 1977: 141). The age at sexual maturity is then given by \(-b_1/b_2\).

Read (1990: Table 2) reports the proportion of individuals that are mature, for ages 1–7 yr. We added 0.5 to the ages (which start at 0) to get the midpoint of the age class, and estimated \( b_1 \) and \( b_2 \) by weighted least squares. The resulting values \( b_1 = -4.7018 \), \( b_2 = 1.3570 \) give an estimated age at sexual maturity of 3.46 yr, which agrees well with the value of 3.44 yr reported by Read (1990).

We estimated the uncertainty in our estimate of age at sexual maturity by bootstrapping the data on survival. The sample at age \( x \) has \( n_i(x) \) immature and \( n_m(x) \) mature individuals in a total sample of \( N(x) = n_i(x) + n_m(x) \). For each age \( x \), we drew a bootstrap sample of size \( N(x) \), with replacement, from the observed sample. We fit the logistic regression to this bootstrap sample and calculated the resulting age at sexual maturity, and repeated this for 2000 samples. Adding the gestation period (~1 yr) gives the distribution of AFR values shown in Fig. 1.

**Harbor Porpoise Vital Rates and Their Uncertainty**

The harbor porpoise is one of the smallest cetaceans, and has evolved a life history that features early reproduction and relatively high fecundity (Read 1990, Read and Hohn 1995). In the Gulf of Maine, most females reach sexual maturity at three years of age and reproduce annually thereafter. Females bear a single calf in May and ovulate and conceive in late June; thus, they are simultaneously lactating and pregnant for much of the year. This intensive reproductive schedule is accompanied by relatively high rates of mortality; the oldest animals found among ~600 specimens taken in herring weirs and gillnets in the Gulf of Maine and Bay of Fundy were 17 yr old (Read and Hohn 1995).

Information on harbor porpoise demography is extremely limited. Estimates of ages and pregnancy rates are available from samples of animals killed in fisheries and from strandings, but there are essentially no data on survival.

Two previous studies have attempted to estimate the rate of increase (Barlow and Boveng 1991, Woodley and Read 1991). In the absence of data on survival, both relied on model life tables (Coale and Demeny 1966); i.e., they used life tables for other species, adapted in ways that would plausibly make them fit the harbor porpoise. Barlow and Boveng (1991) fitted a five-parameter model (Siler 1979) to survivorship curves for fur seals, old-world monkeys, and humans. They rescaled these curves by estimates of maximum longevity (operationally defined as the 99th percentile of the observed age distribution) for the harbor porpoise, and combined them with estimated reproductive rates to calculate the rate of increase \( \lambda \). They obtained values of \( \lambda = 0.917, 0.989, \) and 1.094 for survivorship curves derived from fur seals, old-world monkeys, and humans, respectively.

Woodley and Read (1991) used a survivorship curve for the Himalayan thar (Hemitragus jemlahicus) as a model life table for harbor porpoise. The life histories of thar and harbor porpoises were considered similar enough that no rescaling was done. The resulting value of \( \lambda \) depended on the value assumed for the calf mortality rate; they found \( \lambda \approx 1.04 \), using the minimum calf mortality rate considered realistic.

In this study, we have also used a model life table approach, but have set more rigorous standards for how similar to the harbor porpoise a species must be to be included. We have also used more species as models, enabling us to use Monte Carlo sampling to estimate the uncertainty in this crude estimate of survival, and to combine it with the uncertainty in the other vital rates.

**Maturity and fertility**

The age at first reproduction (AFR) is an important quantity in our calculations, because we use it to adjust the time scale of the life cycles of other species to match that of the harbor porpoise. There are several ways of estimating age at first reproduction (DeMaster 1984). Of these, we chose to estimate age at sexual maturity as the age at which 50% of the population has matured, and AFR as the age at sexual maturity plus an approximate gestation period.

We estimated age at sexual maturity by fitting a logistic regression to the proportion \( p(x) \) of individuals mature at age \( x \):

\[
\frac{p(x)}{1-p(x)} = \exp(b_1 + b_2x).
\]

We estimated \( b_1 \) and \( b_2 \) by weighted least squares (Chatterjee and Price 1977: 141). The age at sexual maturity is then given by \(-b_1/b_2\).

Read (1990: Table 2) reports the proportion of individuals that are mature, for ages 1–7 yr. We added 0.5 to the ages (which start at 0) to get the midpoint of the age class, and estimated \( b_1 \) and \( b_2 \) by weighted least squares. The resulting values \( b_1 = -4.7018 \), \( b_2 = 1.3570 \) give an estimated age at sexual maturity of 3.46 yr, which agrees well with the value of 3.44 yr reported by Read (1990).

We estimated the uncertainty in our estimate of age at sexual maturity by bootstrapping the data on survival. The sample at age \( x \) has \( n_i(x) \) immature and \( n_m(x) \) mature individuals in a total sample of \( N(x) = n_i(x) + n_m(x) \). For each age \( x \), we drew a bootstrap sample of size \( N(x) \), with replacement, from the observed sample. We fit the logistic regression to this bootstrap sample and calculated the resulting age at sexual maturity, and repeated this for 2000 samples. Adding the gestation period (~1 yr) gives the distribution of AFR values shown in Fig. 1.
Read (1990) also reported age-specific pregnancy rates and sample sizes for harbor porpoises killed as by-catch in the Gulf of Maine. We divided these rates by two to estimate birth rate \( m_i \) one year later (Table 2). This assumes a sex ratio of unity, and that all observed pregnancies are carried to term. We describe the uncertainty in the birth rates by treating each age-specific rate as a binomial random variable with the specified sample size.

### Survival

Survival can be estimated directly from repeated observations of marked individuals, or, with appropriate assumptions, from estimates of the age distribution. There are no data on marked individuals for harbor porpoises used for the model life-tables. To estimate the uncertainty in harbor porpoise survival, we sampled this space by combining the model life tables. These distributions are summarized in Table 3. The coefficient of variation of AFR is on the order of 1–5% for well-documented species such as the pilot whale, orca, and the wildebeest, and on the order of 5–10% for species such as the Dall sheep, impala, and zebra, for which little information was available.

#### Monte Carlo uncertainty estimation

Fig. 3 shows an example of the rescaled survivorship curves for the nine species; they span a wide range of mortality patterns. We expect that the harbor porpoise survival schedule falls somewhere in this space of model life tables. To estimate the uncertainty in harbor porpoise survival, we sampled this space by combining the model life tables at random, according to the following algorithm (Fig. 2):  

1. Select at random a value of harbor porpoise age at first reproduction, AFR\(\text{H} \), from the distribution shown in Fig. 1.  
2. Select at random a value of AFR, for model species \( i \), from the appropriate distribution.  
3. Rescale the time for model species \( i \), according to Eq. 2 to obtain \( T^*_i \), and generate a rescaled survivorship curve \( l(x) \). From this curve, calculate the survival probabilities \( P_{ij}^0 = l(j)/l(j - 1) \) for each age class \( j \) of species \( i \), assuming a birth-pulse model with post-breeding census (Caswell 1989).

Let \( T^* \) denote the time scale for model species \( i \). We rescale time for species \( i \) by

\[
T^*_i = \frac{AFR_H}{AFR_i}
\]

where AFR\(\text{H} \) is the age at first reproduction for harbor porpoise. Thus, for example, a single year in the life of a killer whale, with a typical AFR on the order of 15 yr, corresponds to a little less than one-third of a year in the life of a harbor porpoise with a typical AFR on the order of 4 yr.

Our estimates of AFR and its uncertainty varied from species to species, depending on the information available. The appendix details sources of the data and the calculations. The end result of these computations is a set of distributions that characterize the uncertainty in knowledge of the AFR of the species used for the model life tables. These distributions are summarized in Table 3. The coefficient of variation of AFR is on the order of 1–5% for well-documented species such as the pilot whale, orca, and the wildebeest, and on the order of 5–10% for species such as the Dall sheep, impala, and zebra, for which little information was available.

### Table 3

Species used in model life table construction, with the mean, standard deviation, and coefficient of variation of age at first reproduction (AFR).

<table>
<thead>
<tr>
<th>Species</th>
<th>Age at first reproduction (yr)</th>
<th>Mean</th>
<th>sd</th>
<th>cv</th>
</tr>
</thead>
<tbody>
<tr>
<td>Harbor porpoise</td>
<td>4.50</td>
<td>0.292</td>
<td>0.065</td>
<td></td>
</tr>
<tr>
<td>Dall sheep</td>
<td>2.00</td>
<td>0.206</td>
<td>0.103</td>
<td></td>
</tr>
<tr>
<td>Wildebeest</td>
<td>2.24</td>
<td>0.101</td>
<td>0.045</td>
<td></td>
</tr>
<tr>
<td>Elephant</td>
<td>13.17</td>
<td>0.615</td>
<td>0.047</td>
<td></td>
</tr>
<tr>
<td>Impala</td>
<td>2.00</td>
<td>0.203</td>
<td>0.102</td>
<td></td>
</tr>
<tr>
<td>Buffalo</td>
<td>4.00</td>
<td>0.204</td>
<td>0.051</td>
<td></td>
</tr>
<tr>
<td>Zebra</td>
<td>3.00</td>
<td>0.194</td>
<td>0.065</td>
<td></td>
</tr>
<tr>
<td>Orca</td>
<td>14.50</td>
<td>0.480</td>
<td>0.033</td>
<td></td>
</tr>
<tr>
<td>Ringed seal</td>
<td>5.86</td>
<td>0.377</td>
<td>0.064</td>
<td></td>
</tr>
<tr>
<td>Pilot whale</td>
<td>8.93</td>
<td>0.147</td>
<td>0.016</td>
<td></td>
</tr>
</tbody>
</table>

Let \( T^*_i = \frac{AFR_H}{AFR_i} \), and generate a rescaled survivorship curve \( l(x) \). From this curve, calculate the survival probabilities \( P_{ij}^0 = l(j)/l(j - 1) \) for each age class \( j \) of species \( i \), assuming a birth-pulse model with post-breeding census (Caswell 1989).

---

**Table 2.** Age-specific birth rate \( m_i \) for the harbor porpoise, obtained from data of Read (1990) on the age-specific pregnancy rate of animals taken as by-catch in the Gulf of Maine.

<table>
<thead>
<tr>
<th>Age (yr)</th>
<th>( m_i )</th>
<th>( N )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.00</td>
<td>19</td>
</tr>
<tr>
<td>2</td>
<td>0.00</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>0.136</td>
<td>22</td>
</tr>
<tr>
<td>4</td>
<td>0.417</td>
<td>12</td>
</tr>
<tr>
<td>5</td>
<td>0.818</td>
<td>11</td>
</tr>
<tr>
<td>6</td>
<td>0.714</td>
<td>7</td>
</tr>
<tr>
<td>( \geq 7 )</td>
<td>0.833</td>
<td>6</td>
</tr>
</tbody>
</table>
4) Repeat steps 2–3 for all nine species.

5) For each age \( j \), treat the nine values of survival probability as a distribution of possible values for the harbor porpoise. Draw one of these at random and use it as the survival probability at age \( j \) for the harbor porpoise.

The random selection of one of the survival probabilities was based on the following rules. With probability \( q \), the survival probability for age \( j \) was obtained from the same species used at age \( j - 1 \). With probability \( 1 - q \), survival probability at age \( j \) was obtained from a species chosen at random from one of the species not used at age \( j - 1 \). If \( q = 1 \), each life table is treated as a unit, and the sampling consists of picking a model species at random and using its life table. At the other extreme, if \( q = 1/9 \), survival probabilities are sampled randomly at each age, independently of the species providing the survival probability at the previous age. Thus, \( q \) is a way to examine the effect of correlations among age-specific survival values within species.

6) Repeat steps 1–5 many times, each time generating a new harbor porpoise survival schedule from within the space of our nine model survival schedules.

Fig. 4 shows samples of the survivorship curves computed in this way. The tendency for the curves to cluster into species groups is evident when \( q = 1 \).

**Constructing demographic models**

The Monte Carlo procedure previously described generates a set of age-specific survival probabilities. These were combined, as shown in Fig. 2, with a set of reproductive output \( (m_i) \) values obtained by binomial sampling of the observed distribution of age-specific pregnancy rates. (Because the reproductive data are
already expressed on the harbor porpoise time scale, no rescaling is necessary.) These values were combined into an age-classified projection matrix

\[
A = \begin{pmatrix}
F_1 & F_2 & F_3 & \cdots \\
0 & 0 & 0 & \cdots \\
0 & P_2 & 0 & \cdots \\
\vdots & \vdots & \vdots & \ddots 
\end{pmatrix}
\]

(3)

where the age-specific fertility term \( F_i = P_i m_i \), assuming a postbreeding census (Caswell 1989).

Population growth rate was calculated as the dominant eigenvalue \( \lambda \) of the matrix \( A \). This process was repeated 2000 times to give a distribution of \( \lambda \) incorporating uncertainty in the AFR for harbor porpoise, uncertainty in AFR for each of the species used in construction of the model life table, uncertainty in the location of the harbor porpoise survivorship schedule within the space of survivorships of other similar mammals, and uncertainty in harbor porpoise fertilities.

**RESULTS**

**Rate of increase and its uncertainty**

The uncertainty in population growth rate is shown in the probability distribution of \( \lambda \) (Fig. 5), for \( q = 1/9 \) (random selection of model species survivals at each age), \( q = 1 \) (each species life table treated as a unit), and an intermediate value of \( q = 0.5 \). The value of \( q \) does not have a large effect on the results. The distribution of \( \lambda \) values for \( q = 1 \) is more variable, because when \( q < 1 \) some of the interspecies variability in survival is averaged out.

The percentiles of the distribution are given in Table 4. The median values of \( \lambda \) range only from 1.096 to 1.111, depending on the value of \( q \). The means are even more similar (1.0914, 1.0932, 1.0915). The median and mean values are close to the highest of the three model life table estimates (\( \lambda = 1.094 \)) of Barlow and Boveng (1991). Woodley and Read’s (1991) model life table estimate of 1.04 corresponds to about the 8th,
Table 4. Percentiles of the distribution of \( \lambda \) (rate of increase) for harbor porpoise, based on 2000 samples. Results are shown for \( \lambda \) under three values of \( q \).

<table>
<thead>
<tr>
<th>Percentile</th>
<th>( q = 1/9 )</th>
<th>( q = 0.5 )</th>
<th>( q = 1 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.01</td>
<td>1.0187</td>
<td>1.0009</td>
<td>0.9598</td>
</tr>
<tr>
<td>0.05</td>
<td>1.0346</td>
<td>1.0280</td>
<td>0.9789</td>
</tr>
<tr>
<td>0.10</td>
<td>1.0438</td>
<td>1.0399</td>
<td>0.9906</td>
</tr>
<tr>
<td>0.25</td>
<td>1.0653</td>
<td>1.0646</td>
<td>1.0325</td>
</tr>
<tr>
<td>0.50</td>
<td>1.0956</td>
<td>1.0957</td>
<td>1.1108</td>
</tr>
<tr>
<td>0.75</td>
<td>1.1173</td>
<td>1.1252</td>
<td>1.1426</td>
</tr>
<tr>
<td>0.90</td>
<td>1.1326</td>
<td>1.1407</td>
<td>1.1698</td>
</tr>
<tr>
<td>0.95</td>
<td>1.1399</td>
<td>1.1489</td>
<td>1.1826</td>
</tr>
<tr>
<td>0.99</td>
<td>1.1536</td>
<td>1.1623</td>
<td>1.1916</td>
</tr>
</tbody>
</table>

10th, and 29th percentile, depending on the value of \( q \). This is also the value of \( \lambda \) adopted by the National Marine Fisheries Service as a default value to be used in Potential Biological Removal calculations for cetacean stocks for which no other estimates are available (Barlow et al. 1995).

Based on these results, we conclude that, unless the vital rates for the harbor porpoise are unusual among large, monovular mammals, potential population growth rates greater than about 14–18% per year are unlikely. Values of about 10% seem much more plausible. We also note that \( \lambda \) is estimated with considerable uncertainty. 90% confidence intervals (the range between the 5th and 95th percentiles) are 1.03–1.14 for \( q = 1/9 \); 1.03–1.15 for \( q = 0.5 \); and 0.98–1.18 for \( q = 1 \).

Incidental mortality and its uncertainty

Bravington and Bisack’s (1996) estimates of U.S. by-catch in the Gulf of Maine are based on a shipboard observer program and estimates of total landings in the fishery. The by-catch was significantly lower in 1992 and 1993 than in 1990; no other between-year differences were significant. They used a bootstrap procedure to generate confidence intervals for by-catch in each year.

Trippel et al. (1996) provide estimates of Canadian by-catch in the Bay of Fundy, also based on an observer program. In 1993, \(424 \pm 224 \) individuals (mean \( \pm \) 1 SE) were killed. In 1994, the estimate was 101, with a 95% confidence interval from 80 to 122 individuals. They do not explain why they report a standard error in one year and a confidence interval in the other.

There are two sources of uncertainty in these estimates: variability from year to year and sampling uncertainty within the year. We combined these in our Monte Carlo procedure by treating the estimate as a stratified sampling problem. We generated a number for the U.S. by-catch by picking at random a year from the four years for which we have data (1990–1993), and then picking a value from the bootstrap distribution for that year. This is equivalent to drawing a single value from the pooled bootstrap distributions for the four years (Fig. 6). We did the same for the Canadian by-catch, randomly selecting a year and then drawing a value from a triangular distribution on the interval appropriate for that year (200–648 in 1993, 80–122 in 1994). The distribution for the Canadian by-catch is shown in Fig. 7. We add the two numbers together to get a total by-catch estimate \( K \).

The incidental mortality rate \( M = K/N \) is generated by dividing the by-catch value by a population size \( N \), drawn at random from the bootstrap distribution for population size (see Fig. 8) in Smith et al. (1993).

The resulting distribution for the mortality rate \( M \) is shown in Fig. 9. The mean of \( M \) is 0.0495, and the median is 0.0419, but the distribution is skewed to the right and contains considerable variability (a 95% confidence interval ranges from 0.0186 to 0.1119).
Mortality compared with the rate of increase

We have, finally, two quantities: the population growth rate $\lambda$, and the incidental mortality rate $M$, each measured with uncertainty characterized by a distribution of values. We compared $M$ with the yearly growth rate, calculated as $R = \lambda - 1$. Doing this repeatedly, we calculated the probability that the by-catch mortality rate $M$ exceeds each of four threshold values:

1) The value $R$, which represents a theoretical upper bound to the mortality rate that the population can possibly sustain.

2) The value $R/2$, which is recommended by the International Whaling Commission (IWC 1991) as an upper limit to the combined rates of harvest and incidental mortality. This is the maximum possible critical value under the Marine Mammal Protection Act; it would result from setting the recovery factor to its maximum value (1.0) and from knowing the population size with absolute certainty.

3) The value $R/4$, recommended by the International Whaling Commission (IWC 1996) as a rate sufficient to be cause for concern about incidental mortality. This would be the Marine Mammal Protection Act critical value, given the recovery factor of 0.5, if actual population size, rather than the minimum population size, were used in the calculation.

4) The value $0.2134R$, which is the current critical value for this stock under the Marine Mammal Protection Act, given the recovery factor of 0.5 and using the 20th percentile of a lognormal distribution as an estimate of minimum population size.

Results are shown in Table 5. They are sensitive to the value of $q$, but not dramatically so. Taking into account what is known, and acknowledging what is unknown about harbor porpoise demography, the probability that incidental mortality exceeds the International Whaling Commission recommendation of $R/4$ is at least 0.8. The probability that it exceeds the threshold for classification as a strategic stock under the Marine Mammal Protection Act ranges from 0.88 to 0.94, depending on the value of $q$. There is about an even chance (probability from 0.46 to 0.51) that it exceeds the maximum possible threshold ($R/2$) under the Marine Mammal Protection Act. The probability that it exceeds $R$, leaving no margin for safety at all, is at least 0.166.

Discussion

Critical values of incidental mortality of the harbor porpoise range downward from one-half the potential rate of increase (IWC 1991) to one-fourth that rate (IWC 1996) to roughly one-fifth that rate under the Marine Mammal Protection Act. The probabilities that these critical values are exceeded range from about 0.5 to 0.95 (Table 5). Thus, it is very likely under international standards, and almost certain under U.S. standards, that the level of harbor porpoise by-catch in this population is too high. We conclude that the available evidence, fragmentary and uncertain as it is in some areas, indicates that the harbor porpoise is at risk from recent levels of incidental mortality in sink gillnet fisheries in the Gulf of Maine and the Bay of Fundy.

**Table 5.** Probabilities (Pr) that incidental mortality exceeds critical values, defined relative to the population growth rate. Values are given for $q = 1/9$, $q = 0.5$, and $q = 1$. $R = \lambda - 1$ denotes the yearly growth rate.

<table>
<thead>
<tr>
<th>Probabilities</th>
<th>$q = 1/9$</th>
<th>$q = 0.5$</th>
<th>$q = 1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pr ($M \geq R$)</td>
<td>0.1660</td>
<td>0.1895</td>
<td>0.3030</td>
</tr>
<tr>
<td>Pr ($M \geq R/2$)</td>
<td>0.5055</td>
<td>0.4820</td>
<td>0.4640</td>
</tr>
<tr>
<td>Pr ($M \geq R/4$)</td>
<td>0.8850</td>
<td>0.8705</td>
<td>0.7990</td>
</tr>
<tr>
<td>Pr ($M \geq 0.2134R$)</td>
<td>0.9400</td>
<td>0.9245</td>
<td>0.8795</td>
</tr>
</tbody>
</table>
Incidental mortality rates for the harbor porpoise have also been estimated in other parts of the world. Hammond (1995) reports rates of 3–5% per year in the North Sea and the Celtic Shelf, and Carlstrom and Berggren (1995) report a rate of 2.9% in the Skagerrak Sea off Sweden. These rates are comparable to the values in the Gulf of Maine. We have not carried out uncertainty calculations for these populations, because we have no information on the uncertainty in the estimates of by-catch and population size. However, because we expect the biology of harbor porpoises to be similar in these populations, we believe that there is cause for concern in these populations as well.

The results of our analysis are probabilities, not yes-or-no answers. This raises the question of how high such a probability must be before it warrants management action. The most optimistic of the results in Table 5 is that incidental mortality exceeds \( R \), without any safety margin, with a probability of 0.166. Is this a dangerously high probability, or a reassuringly low one? Note that this is also the probability of losing a round of Russian roulette. Most people would say that accepting these odds and pulling the trigger is reckless behavior, because the consequences are so extreme. The consequence of incidental mortality that exceeds the potential growth rate is eventual extinction.

Of course, this analogy cannot be pursued too far. The consequences of losing at Russian roulette are immediate and irreversible, whereas extinction takes time. Nonetheless, the high probabilities that incidental mortality exceeds all the criteria considered, even that without a safety margin, are cause for immediate concern.

**Sources of uncertainty**

Much of our effort in this paper is directed at estimating \( \lambda \), because the lack of data on survival of the harbor porpoise has forced us to a novel use of model life tables. Given this situation, our estimate of \( \lambda \) has much more uncertainty than that estimated for the killer whale by Brault and Caswell (1993), based on the best set of demographic data for any cetacean. But, how does the uncertainty in \( \lambda \) compare with that in the other quantities \((N \text{ and } K)\) appearing in our final calculations? One way to quantify the relative precision of an estimate is the coefficient of variation (CV; the ratio of the standard deviation to the mean). The CV of \( \lambda \), depending on the value of \( q \), ranges from 0.031 to 0.061. This is much less than the CV of by-catch (0.470) or of population size (0.230; based on the bootstrap distribution) or of the incidental mortality rate (0.521). Thus, the aspect of this problem about which we know the least is not harbor porpoise demography, but incidental mortality rate, and within that, the amount of by-catch.

Parameter estimation is not the only source of uncertainty. Our results also depend on our underlying conjecture that the survival probabilities for the harbor porpoise lie somewhere in the space spanned by the survival schedules of other large mammals with similar life histories. If this conjecture is incorrect—if, unbeknownst to us, the harbor porpoise were unique among mammals in having the survivorship curve of a clam, for example—our results would not capture anything like the true value of \( \lambda \) for the harbor porpoise.

One way to assess the quality of our description of harbor porpoise demography is to compare the age distributions predicted by the model with the (admittedly limited) age distribution data. Read and Hohn (1995) conclude that “harbor porpoises are clearly capable of living to ages of 20 yr or more, but individuals seldom reach such advanced age.” The oldest animals found in over 600 individuals from the Gulf of Maine and Bay of Fundy were two 17-yr-olds. In a sample of 200 individuals from California, the oldest individual was 24 yr old.
Fig. 10 shows the proportion of the population over 20 yr old predicted by the stable age distribution from a sample of 1000 randomly generated sets of harbor porpoise demographic parameters. Regardless of the value of $q$, the median proportion is about 0.012. These stable age distributions are calculated assuming no incidental mortality. Incidental mortality, even if independent of age, will result in even fewer old individuals. Thus, the observed oldest animals are not inconsistent with the age distributions implied by our use of model life tables.

The implementation of management strategies can also introduce uncertainty. Rosenberg and Brault (1993) studied the effects of reduced fishing mortality on stock recovery in a model of yellowtail flounder. Uncertainty in the impact of regulations on the actual fishing mortality changed the pattern of stock recovery and the probability that the intervention would meet its goals of reducing yield.

The interpretation of uncertainty

Our approach treats uncertainty in the same way that classical statistics treats sampling error; it yields the uncertainty of an estimate of $\lambda$, where $\lambda$ is viewed as a fixed, but unknown, parameter. If we knew more (having larger samples or better data), the uncertainty would be less, just as the standard error of the estimate of a mean decreases with increasing sample size.

As for most statistical calculations, there exists a Bayesian alternative to this interpretation, in which the parameters are treated as random variables whose distribution depends on prior subjective knowledge. Bayes’ formula is used to update the distribution as additional data are obtained. To a Bayesian, our distribution of $\lambda$ would be a posterior distribution, the result of applying our information on the harbor porpoise (the data on AFR and reproductive rates, the characteristics of the porpoise life history, the available life tables for mammal species with similar life histories) to a non-informative prior distribution expressing our ignorance about the vital rates of the harbor porpoise. There is currently considerable interest in (Raffery et al. 1995, Taylor et al. 1996) and controversy about (Dennis 1996) Bayesian methods in ecology, but we leave the development of a Bayesian version of our results as an open problem.

Uncertainty in an estimate should not be confused with stochastic variation in demographic rates over time. We do not consider effects of stochastic temporal variation here, because we have no information on such variation. If we did, we could calculate stochastic population statistics (e.g., long-term growth rates, extinction probabilities; see Tuljapurkar 1990). These statistics would be uncertain because of uncertainty in the parameters of the stochastic models, and that uncertainty could be addressed using the methods we adopt here.

We have shown that it is possible to incorporate uncertainty into even complicated demographic calculations, and to map that uncertainty into the results of those calculations. In the case of the harbor porpoise, we provide strong support for the conclusion that incidental mortality rates exceed the levels recommended by national and international management agencies. It remains to be seen what actions will be taken to ameliorate the situation.

Acknowledgments

We thank Myriam Barbeau, Jay Barlow, Yoh Iwasa, Roger Powell, Bonnie Ripley, Barb Taylor, and two reviewers for comments on previous versions of this paper, and Mark Bravington, Kathryn Bisack, and Debbie Palka for providing results from their bootstrap procedures. This research was supported by NSF Grant DEB-9211945 to H. Caswell, and NMFS Cooperative Agreement NA57FL0557 to A. Read and S. Brault. This is Woods Hole Oceanographic Institution Contribution 9237.

Literature Cited


APPENDIX

AFR AND SURVIVORSHIP CALCULATIONS FOR MODEL LIFE TABLE SPECIES

This Appendix summarizes the sources of data and analytical procedures used to estimate age at first reproduction and survivorship for each of the nine species used for model life tables. We have tried to be sufficiently precise in our descriptions that the interested reader could repeat the calculations.

In this appendix, ASM denotes age at sexual maturity, and AFR age at first reproduction.

Pilot whale (Globicephala melas).—Bloch et al. (1993) estimated the median age at sexual maturity as 8.1 yr from a sample of 283 female pilot whales (aged 4–12 yr) taken in the Faroese drive fishery. They do not provide any information on sample sizes for individual ages, so we divided the 283 individuals evenly among the eight age classes. We estimated the proportions of mature whales from Bloch et al. (1993; Fig. 11). Fitting a logistic regression to these data estimated the proportions of mature whales from Bloch et al. (1993) (Sanders-Reed 1996). It gives values similar to the nonparametric fit described in Bloch et al. (1993; Table 6), but gives a significantly better fit.

Killer whale (Orcinus Orca).—Olesiuk et al. (1990: Table 6) give sample sizes and the number of individuals that have reproduced for ages 10–18 yr. These data refer to first reproduction, not sexual maturity, so there is no need to add the gestation time to the estimate. Olesiuk et al. (1990) report a median AFR of 14.40 yr. Our logistic regression gives $b_1 = -10.968$, $b_2 = 1.3637$, $ASM = 8.042$, which is in close agreement with the values reported by Bloch et al. (1993; $b_1 = -10.070$, $b_2 = 1.249$, $ASM = 8.1$). We generated a distribution of values for AFR by the bootstrap procedure described for the harbor porpoise, adding a gestation period of 326 d (Bloch et al. 1993) to the ASM values.

The survivorship curve for the pilot whale was based on a nonparametric fit to the age distribution data in Bloch et al. (1993) (Sanders-Reed 1996). It gives values similar to the Siler model fit described in Bloch et al. (1993: Table 6), but gives a significantly better fit.

African elephant (Loxodonta africana).—The age at first reproduction in the elephant is sensitive to density (Laws 1973). Because we are trying to generate a potential population growth rate for the harbor porpoise, we chose data from Laws (1973: Fig. 1) for a low-density population (Mkomasi). This gives a median age at sexual maturity of 12.3 yr (with a 95% confidence interval of [10.62, 13.33]). We added 1 yr to obtain an AFR of 13.5 yr. To describe the uncertainty in the estimate, we used a triangular distribution with support on the 95% confidence interval; i.e., from 11.62 to 14.33 yr.

Survivorship information for the African elephant was obtained from Olesiuk et al. (1990: Table 6) give sample sizes and the number of individuals that have reproduced at age 2 yr; 40 out of 48 reproduced at age 3 yr; and 86 out of 90 reproduced at ages ≥4 yr. No 1-yr-old cows reproduced, but Watson does not report the sample size, so we assumed a sample size of 50 as a value similar to that for the other ages. Logistic regression gives $b_1 = -3.5030$, $b_2 = 1.5733$, and AFR = 2.227 years. We calculated the uncertainty in this estimate by the bootstrap procedure described for the harbor porpoise.

Survivorship data for the impala were taken from Simmons et al. (1984: Table 2). Dassie (1979) gives reproductive output figures as a function of age. By age 2 yr, reproduction has reached about 50% of its maximum value, which suggests using 2 years as a median AFR. In the absence of any information on which to calculate uncertainty, we used a triangular distribution on the interval [1.5, 2.5]. Survivorship data for the impala were taken from Simmons et al. (1984: Table 2).

Ringed seal (Phoca hispida).—Smith (1975: Table 55) gives sample sizes and proportion of individuals mature for ages 4–10 yr. We fit a logistic regression to these data and obtained $b_1 = -3.793$, $b_2 = 0.7713$, and ASM = 4.92 years. We calculated the uncertainty in age at sexual maturity using the bootstrap procedure described for the harbor porpoise, and added 1 yr to the resulting figure to obtain a distribution of AFR. Survivorship data for the ringed seal were taken from the composite life table in Smith (1975: Table 61). Western (1979) gives the age at first reproduction as 2 yr. In the absence of any other information, we used a triangular distribution on the interval [1.5, 2.5] to describe the uncertainty in AFR. Survivorship data for the impala were taken from the female life table in Spinage (1972: Table 4).

Zebra (Equus burchelli).—Western (1979) gives the mean age at first reproduction as 3 yr. In the absence of any other information, we used a triangular distribution on the interval [2.5, 3.5] to describe the uncertainty in AFR. Survivorship data for the zebra were taken from the female life table in Spinage (1972: Table 6).

African buffalo (Syncerus caffer).—Western (1979) gives the mean age at first reproduction as 4 yr. In the absence of any other information, we used a triangular distribution on the interval [3.5, 4.5] to describe the uncertainty in AFR. Survivorship data for the African buffalo were taken from the female life table in Spinage (1972: Table 5).