Bias of Maximum Age Estimators of Natural Mortality

Paul Rago

National Marine Fisheries Service
Northeast Fisheries Science Center
166 Water Street, Woods Hole, MA
ABSTRACT

Estimates of natural mortality based on maximum age are biased because the maximum age is a random variable whose value is influenced by the total mortality on the population. Even in rare instances when the total mortality rate can be assumed to be attributable solely to natural mortality, the maximum age will be biased if a fixed detection criterion is applied. Regression estimators of total mortality have less bias than maximum age and do not require the additional assumption of a detection criterion. Simple examples illustrate that maximum age estimators are nearly useless when total mortality has a non negligible component of fishing mortality.
Introduction

The maximum age observed in a sample is often used as a measure of natural mortality. In unfished or lightly fished populations this measure has relevance since the oldest fish in a sample of size \( n \) suggests that it is possible to live to be at least \( A \) years old given the total force of mortality \( = Z \times A \) where \( Z \) is the total instantaneous rate of mortality applied to the population annually. To obtain an estimate of natural mortality the oldest aged fish in a sample is hypothesized to represent some arbitrary fraction of its original cohort, which can be denoted as \( \alpha \). Often \( \alpha \) is assumed to range from 0.01 to 0.03 but sample size \( n \) in which the fish of age \( A \) is found is not considered. In the following example I consider the sampling properties of maximum age estimator of natural mortality and consider more robust estimate based on a catch curve.

Methods

Assume that the dynamics of a population are governed by simple exponential decay process in which the instantaneous rate of total mortality is denoted by the variable \( Z \). The number of individuals alive at age \( a \) will be determined by

\[
N_a = N_0 e^{-Za} \tag{1}
\]

The fraction of the original population alive as age \( a \) is denoted as \( \alpha \) and is simply defined as \( N_a / N_0 \). Dividing both sides of Eq. 1 by \( N_0 \) and solving for \( Z \) yield the rate of annual mortality corresponding to the observation of fish of age \( a \) and a detection criterion \( \alpha \). If we denote the maximum age observed as \( A \) then Eq. 1 becomes:

\[
Z = -\ln(\alpha) / A \tag{2}
\]

Since \( Z \) is defined as the sum of the instantaneous rates of natural mortality \( M \) and fishing mortality \( F \), it is clear that \( Z \) will become a less biased measure of \( M \) as \( F \) approaches zero. Similarly the magnitude of \( Z \) will be 31\% greater when \( \alpha = 0.01 \) than when \( \alpha = 0.03 \). If \( \alpha \) is chosen arbitrarily then the estimate of \( M \) will decline sample size increases. This is expected since the likelihood of finding the oldest true age in the population will increase as the sample size \( n \) approaches an enumeration of the true population size.

One way of incorporating the effect of sample size in the estimator of \( Z \) is to assume that a population is at equilibrium with a constant rate of recruitment, denoted as \( N_0 \). The expected age distribution of fish in the population is then defined as

\[
P(a) = \frac{N_a}{\sum_{a=1}^{A} N_a} = \frac{e^{-2a}}{\sum_{a=1}^{A} e^{-2a}} \tag{3}
\]

The expected age frequency of fish age \( a \) in a sample of size \( n \) is denoted as \( n_a \) and defined as \( n_a = nP(a) \).

A less arbitrary definition of the maximum expected age \( A \) in a sample of size \( n \) can now be defined as the oldest fish with a probability of at least \( 1/n \). This is still an arbitrary cut point since observations of ages with probabilities less than \( 1/n \) are certainly possible. However specification of the threshold of \( \alpha = 1/n \) relates the maximum age to the number
of random samples. This definition of \( \alpha \) does suffer from the perennial problem of defining the effective number of samples from a population. It is expected to be much less than the actual number of fish measured. For the sake of this exercise it is assumed that the effective sample size is known and that the true maximum age is 50 years. As a comparison between the maximum age estimators with other options, estimates of \( Z \) were computed by applying simple catch curves to the truncated series of observations. In other words, the regression of log C vs age was truncated at age \( A \) where \( P(A) \leq 1/n \). To address the effect of sample size, the expected value of log C was rounded to the nearest integer.

**Results**

The maximum age corresponding to a given detection fraction \( \alpha \) and assumed level of \( Z \) is shown in Table 1 which simply defines \( A = -\ln(\alpha)/Z \). Note that the maximum age can vary over a two fold range when \( \alpha \) ranges from 0.01 to 0.10. Tables 2a and 2b expound on this theme demonstrating the additional biases arising from an arbitrary detection ratio \( \alpha \) and unknown fishing mortality rate. The log of the probability density function vs age is depicted in Fig. 1. Expected maximum age in a sample of size \( n \) under different levels of total mortality is depicted in Fig. 2. Note the slow approach to the true maximum age of 50 as total mortality increases. Table 3 provides additional details on maximum age expected for a range of samples from \( n=150 \) to 3600.

Table 4 illustrates the estimated \( Z \) based on maximum age for a detection criterion of \( 1/n \) for a range of samples sizes and true \( Z \) values. The bias of this estimator decreases as total \( Z \) increases. Table 5 uses the same set of maximum ages but applies a detection threshold criterion to all samples regardless of size. Bias increase with \( Z \). Comparison between the maximum age distribution and catch curve estimates of \( Z \) are presented in Table 6. Catch curve estimates of \( Z \) based on the truncated frequencies are unbiased as expected. Regressions based on the rounded frequencies are slightly biased in this sample of 100 fish. Estimates of \( Z \) based on maximum ages are biased but the degree and direction of the bias depends not only on the magnitude of the true \( Z \) but also by the arbitrary selection of the detection threshold.

**Discussion**

Estimates of \( Z \) based on maximum age in a sample are likely to be biased because the maximum age observed depends on the sample size, the unknown contribution of fishing mortality to the total mortality, and true total mortality rate. A regression estimator based on the sample age composition is much more likely to reveal the true total mortality rate. However, the total mortality rate will approximate the natural mortality rate only if the fishing mortality rate can be assumed to be negligible.
Table 1. Expected maximum ages for a hypothesized Z and threshold fraction

<table>
<thead>
<tr>
<th>Detection Threshold</th>
<th>Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.01</td>
<td>46.1</td>
</tr>
<tr>
<td>0.02</td>
<td>39.1</td>
</tr>
<tr>
<td>0.03</td>
<td>35.1</td>
</tr>
<tr>
<td>0.04</td>
<td>32.2</td>
</tr>
<tr>
<td>0.05</td>
<td>30.0</td>
</tr>
<tr>
<td>0.06</td>
<td>28.1</td>
</tr>
<tr>
<td>0.07</td>
<td>26.6</td>
</tr>
<tr>
<td>0.08</td>
<td>25.3</td>
</tr>
<tr>
<td>0.09</td>
<td>24.1</td>
</tr>
<tr>
<td>1</td>
<td>23.0</td>
</tr>
</tbody>
</table>

Table 2a. Estimated maximum age for combinations of F and M at a detection threshold = 0.010

<table>
<thead>
<tr>
<th>M</th>
<th>0.1</th>
<th>0.2</th>
<th>0.3</th>
<th>0.4</th>
<th>0.5</th>
<th>0.6</th>
<th>0.7</th>
<th>0.8</th>
<th>0.9</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>23.02585</td>
<td>23.0</td>
<td>15.4</td>
<td>11.5</td>
<td>9.2</td>
<td>7.7</td>
<td>6.6</td>
<td>5.8</td>
<td>5.1</td>
<td>4.6</td>
<td>4.2</td>
</tr>
<tr>
<td>0.1</td>
<td>23.0</td>
<td>15.4</td>
<td>11.5</td>
<td>9.2</td>
<td>7.7</td>
<td>6.6</td>
<td>5.8</td>
<td>5.1</td>
<td>4.6</td>
<td>4.2</td>
</tr>
<tr>
<td>0.2</td>
<td>15.4</td>
<td>11.5</td>
<td>9.2</td>
<td>7.7</td>
<td>6.6</td>
<td>5.8</td>
<td>5.1</td>
<td>4.6</td>
<td>4.2</td>
<td>3.8</td>
</tr>
<tr>
<td>0.3</td>
<td>11.5</td>
<td>9.2</td>
<td>7.7</td>
<td>6.6</td>
<td>5.8</td>
<td>5.1</td>
<td>4.6</td>
<td>4.2</td>
<td>3.8</td>
<td>3.5</td>
</tr>
<tr>
<td>0.4</td>
<td>9.2</td>
<td>7.7</td>
<td>6.6</td>
<td>5.8</td>
<td>5.1</td>
<td>4.6</td>
<td>4.2</td>
<td>3.8</td>
<td>3.5</td>
<td>3.3</td>
</tr>
<tr>
<td>0.5</td>
<td>7.7</td>
<td>6.6</td>
<td>5.8</td>
<td>5.1</td>
<td>4.6</td>
<td>4.2</td>
<td>3.8</td>
<td>3.5</td>
<td>3.3</td>
<td>3.1</td>
</tr>
<tr>
<td>0.6</td>
<td>6.6</td>
<td>5.8</td>
<td>5.1</td>
<td>4.6</td>
<td>4.2</td>
<td>3.8</td>
<td>3.5</td>
<td>3.3</td>
<td>3.1</td>
<td>2.9</td>
</tr>
<tr>
<td>0.7</td>
<td>5.8</td>
<td>5.1</td>
<td>4.6</td>
<td>4.2</td>
<td>3.8</td>
<td>3.5</td>
<td>3.3</td>
<td>3.1</td>
<td>2.9</td>
<td>2.7</td>
</tr>
<tr>
<td>0.8</td>
<td>5.1</td>
<td>4.6</td>
<td>4.2</td>
<td>3.8</td>
<td>3.5</td>
<td>3.3</td>
<td>3.1</td>
<td>2.9</td>
<td>2.7</td>
<td>2.6</td>
</tr>
<tr>
<td>0.9</td>
<td>4.6</td>
<td>4.2</td>
<td>3.8</td>
<td>3.5</td>
<td>3.3</td>
<td>3.1</td>
<td>2.9</td>
<td>2.7</td>
<td>2.6</td>
<td>2.4</td>
</tr>
<tr>
<td>1</td>
<td>4.2</td>
<td>3.8</td>
<td>3.5</td>
<td>3.3</td>
<td>3.1</td>
<td>2.9</td>
<td>2.7</td>
<td>2.6</td>
<td>2.4</td>
<td>2.3</td>
</tr>
</tbody>
</table>

Table 2b. Estimated maximum age for combinations of F and M at a detection threshold = 0.050

<table>
<thead>
<tr>
<th>M</th>
<th>0.1</th>
<th>0.2</th>
<th>0.3</th>
<th>0.4</th>
<th>0.5</th>
<th>0.6</th>
<th>0.7</th>
<th>0.8</th>
<th>0.9</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>14.9786</td>
<td>15.0</td>
<td>10.0</td>
<td>7.5</td>
<td>6.0</td>
<td>5.0</td>
<td>4.3</td>
<td>3.7</td>
<td>3.3</td>
<td>3.0</td>
<td>2.7</td>
</tr>
<tr>
<td>0.1</td>
<td>15.0</td>
<td>10.0</td>
<td>7.5</td>
<td>6.0</td>
<td>5.0</td>
<td>4.3</td>
<td>3.7</td>
<td>3.3</td>
<td>3.0</td>
<td>2.7</td>
</tr>
<tr>
<td>0.2</td>
<td>10.0</td>
<td>7.5</td>
<td>6.0</td>
<td>5.0</td>
<td>4.3</td>
<td>3.7</td>
<td>3.3</td>
<td>3.0</td>
<td>2.7</td>
<td>2.5</td>
</tr>
<tr>
<td>0.3</td>
<td>7.5</td>
<td>6.0</td>
<td>5.0</td>
<td>4.3</td>
<td>3.7</td>
<td>3.3</td>
<td>3.0</td>
<td>2.7</td>
<td>2.5</td>
<td>2.3</td>
</tr>
<tr>
<td>0.4</td>
<td>6.0</td>
<td>5.0</td>
<td>4.3</td>
<td>3.7</td>
<td>3.3</td>
<td>3.0</td>
<td>2.7</td>
<td>2.5</td>
<td>2.3</td>
<td>2.1</td>
</tr>
<tr>
<td>0.5</td>
<td>5.0</td>
<td>4.3</td>
<td>3.7</td>
<td>3.3</td>
<td>3.0</td>
<td>2.7</td>
<td>2.5</td>
<td>2.3</td>
<td>2.1</td>
<td>2.0</td>
</tr>
<tr>
<td>0.6</td>
<td>4.3</td>
<td>3.7</td>
<td>3.3</td>
<td>3.0</td>
<td>2.7</td>
<td>2.5</td>
<td>2.3</td>
<td>2.1</td>
<td>2.0</td>
<td>1.9</td>
</tr>
<tr>
<td>0.7</td>
<td>3.7</td>
<td>3.3</td>
<td>3.0</td>
<td>2.7</td>
<td>2.5</td>
<td>2.3</td>
<td>2.1</td>
<td>2.0</td>
<td>1.9</td>
<td>1.8</td>
</tr>
<tr>
<td>0.8</td>
<td>3.3</td>
<td>3.0</td>
<td>2.7</td>
<td>2.5</td>
<td>2.3</td>
<td>2.1</td>
<td>2.0</td>
<td>1.9</td>
<td>1.8</td>
<td>1.7</td>
</tr>
<tr>
<td>0.9</td>
<td>3.0</td>
<td>2.7</td>
<td>2.5</td>
<td>2.3</td>
<td>2.1</td>
<td>2.0</td>
<td>1.9</td>
<td>1.8</td>
<td>1.7</td>
<td>1.6</td>
</tr>
<tr>
<td>1</td>
<td>2.7</td>
<td>2.5</td>
<td>2.3</td>
<td>2.1</td>
<td>2.0</td>
<td>1.9</td>
<td>1.8</td>
<td>1.7</td>
<td>1.6</td>
<td>1.5</td>
</tr>
</tbody>
</table>
Table 3. Maximum age as a function of sample size and total mortality Z. Maximum age is based on probability of observation equal to ~1/n. The true maximum age in the population is 50.

<table>
<thead>
<tr>
<th>Sample size</th>
<th>0.1</th>
<th>0.2</th>
<th>0.3</th>
<th>0.4</th>
<th>0.5</th>
<th>0.6</th>
<th>0.7</th>
<th>0.8</th>
<th>0.9</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>23</td>
<td>15</td>
<td>11</td>
<td>9</td>
<td>8</td>
<td>7</td>
<td>6</td>
<td>6</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>150</td>
<td>27</td>
<td>17</td>
<td>13</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>7</td>
<td>6</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>300</td>
<td>34</td>
<td>20</td>
<td>15</td>
<td>12</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>7</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>450</td>
<td>38</td>
<td>23</td>
<td>16</td>
<td>13</td>
<td>11</td>
<td>9</td>
<td>8</td>
<td>7</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>600</td>
<td>41</td>
<td>24</td>
<td>17</td>
<td>14</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>750</td>
<td>43</td>
<td>25</td>
<td>18</td>
<td>14</td>
<td>12</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>900</td>
<td>45</td>
<td>26</td>
<td>19</td>
<td>15</td>
<td>12</td>
<td>11</td>
<td>9</td>
<td>8</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>1050</td>
<td>47</td>
<td>27</td>
<td>19</td>
<td>15</td>
<td>13</td>
<td>11</td>
<td>9</td>
<td>8</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>1200</td>
<td>48</td>
<td>27</td>
<td>20</td>
<td>15</td>
<td>13</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>1350</td>
<td>49</td>
<td>28</td>
<td>20</td>
<td>16</td>
<td>13</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>1500</td>
<td>50</td>
<td>29</td>
<td>20</td>
<td>16</td>
<td>13</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>1650</td>
<td>50</td>
<td>29</td>
<td>21</td>
<td>16</td>
<td>13</td>
<td>12</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>1800</td>
<td>50</td>
<td>29</td>
<td>21</td>
<td>16</td>
<td>14</td>
<td>12</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>1950</td>
<td>50</td>
<td>30</td>
<td>21</td>
<td>17</td>
<td>14</td>
<td>12</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>2100</td>
<td>50</td>
<td>30</td>
<td>21</td>
<td>17</td>
<td>14</td>
<td>12</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>2250</td>
<td>50</td>
<td>31</td>
<td>22</td>
<td>17</td>
<td>14</td>
<td>12</td>
<td>11</td>
<td>9</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>2400</td>
<td>50</td>
<td>31</td>
<td>22</td>
<td>17</td>
<td>14</td>
<td>12</td>
<td>11</td>
<td>9</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>2550</td>
<td>50</td>
<td>31</td>
<td>22</td>
<td>17</td>
<td>14</td>
<td>12</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>2700</td>
<td>50</td>
<td>31</td>
<td>22</td>
<td>17</td>
<td>14</td>
<td>12</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>2850</td>
<td>50</td>
<td>32</td>
<td>23</td>
<td>18</td>
<td>15</td>
<td>12</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>3000</td>
<td>50</td>
<td>32</td>
<td>23</td>
<td>18</td>
<td>15</td>
<td>13</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>3150</td>
<td>50</td>
<td>32</td>
<td>23</td>
<td>18</td>
<td>15</td>
<td>13</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>3300</td>
<td>50</td>
<td>32</td>
<td>23</td>
<td>18</td>
<td>15</td>
<td>13</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>3450</td>
<td>50</td>
<td>33</td>
<td>23</td>
<td>18</td>
<td>15</td>
<td>13</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>3600</td>
<td>50</td>
<td>33</td>
<td>23</td>
<td>18</td>
<td>15</td>
<td>13</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>8</td>
</tr>
</tbody>
</table>
Table 4. Estimated Z based on a 1/n detection criterion and maximum age observed

<table>
<thead>
<tr>
<th>sample size</th>
<th>0.1</th>
<th>0.2</th>
<th>0.3</th>
<th>0.4</th>
<th>0.5</th>
<th>0.6</th>
<th>0.7</th>
<th>0.8</th>
<th>0.9</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>150</td>
<td>0.186</td>
<td>0.295</td>
<td>0.385</td>
<td>0.501</td>
<td>0.557</td>
<td>0.626</td>
<td>0.716</td>
<td>0.835</td>
<td>1.002</td>
<td>1.002</td>
</tr>
<tr>
<td>300</td>
<td>0.168</td>
<td>0.285</td>
<td>0.380</td>
<td>0.475</td>
<td>0.570</td>
<td>0.634</td>
<td>0.713</td>
<td>0.815</td>
<td>0.951</td>
<td>0.951</td>
</tr>
<tr>
<td>450</td>
<td>0.161</td>
<td>0.266</td>
<td>0.382</td>
<td>0.470</td>
<td>0.555</td>
<td>0.679</td>
<td>0.764</td>
<td>0.873</td>
<td>0.873</td>
<td>1.018</td>
</tr>
<tr>
<td>600</td>
<td>0.156</td>
<td>0.267</td>
<td>0.376</td>
<td>0.457</td>
<td>0.582</td>
<td>0.640</td>
<td>0.711</td>
<td>0.800</td>
<td>0.914</td>
<td>1.066</td>
</tr>
<tr>
<td>750</td>
<td>0.154</td>
<td>0.265</td>
<td>0.368</td>
<td>0.473</td>
<td>0.552</td>
<td>0.662</td>
<td>0.736</td>
<td>0.828</td>
<td>0.946</td>
<td>0.946</td>
</tr>
<tr>
<td>900</td>
<td>0.151</td>
<td>0.262</td>
<td>0.358</td>
<td>0.453</td>
<td>0.567</td>
<td>0.618</td>
<td>0.756</td>
<td>0.850</td>
<td>0.972</td>
<td>0.972</td>
</tr>
<tr>
<td>1050</td>
<td>0.148</td>
<td>0.258</td>
<td>0.366</td>
<td>0.464</td>
<td>0.535</td>
<td>0.632</td>
<td>0.773</td>
<td>0.870</td>
<td>0.983</td>
<td>0.994</td>
</tr>
<tr>
<td>1200</td>
<td>0.148</td>
<td>0.263</td>
<td>0.355</td>
<td>0.473</td>
<td>0.545</td>
<td>0.645</td>
<td>0.709</td>
<td>0.788</td>
<td>0.886</td>
<td>1.013</td>
</tr>
<tr>
<td>1350</td>
<td>0.147</td>
<td>0.257</td>
<td>0.360</td>
<td>0.450</td>
<td>0.554</td>
<td>0.655</td>
<td>0.721</td>
<td>0.801</td>
<td>0.901</td>
<td>1.030</td>
</tr>
<tr>
<td>1500</td>
<td>0.146</td>
<td>0.252</td>
<td>0.366</td>
<td>0.457</td>
<td>0.563</td>
<td>0.665</td>
<td>0.731</td>
<td>0.813</td>
<td>0.914</td>
<td>1.045</td>
</tr>
<tr>
<td>1650</td>
<td>0.148</td>
<td>0.255</td>
<td>0.353</td>
<td>0.463</td>
<td>0.570</td>
<td>0.617</td>
<td>0.741</td>
<td>0.823</td>
<td>0.926</td>
<td>1.058</td>
</tr>
<tr>
<td>1800</td>
<td>0.150</td>
<td>0.258</td>
<td>0.357</td>
<td>0.468</td>
<td>0.535</td>
<td>0.625</td>
<td>0.750</td>
<td>0.833</td>
<td>0.937</td>
<td>0.937</td>
</tr>
<tr>
<td>1950</td>
<td>0.152</td>
<td>0.253</td>
<td>0.361</td>
<td>0.446</td>
<td>0.541</td>
<td>0.631</td>
<td>0.758</td>
<td>0.842</td>
<td>0.947</td>
<td>0.947</td>
</tr>
<tr>
<td>2100</td>
<td>0.153</td>
<td>0.255</td>
<td>0.364</td>
<td>0.450</td>
<td>0.546</td>
<td>0.637</td>
<td>0.765</td>
<td>0.850</td>
<td>0.956</td>
<td>0.956</td>
</tr>
<tr>
<td>2250</td>
<td>0.154</td>
<td>0.249</td>
<td>0.351</td>
<td>0.454</td>
<td>0.551</td>
<td>0.643</td>
<td>0.702</td>
<td>0.858</td>
<td>0.965</td>
<td>0.965</td>
</tr>
<tr>
<td>2400</td>
<td>0.156</td>
<td>0.251</td>
<td>0.354</td>
<td>0.458</td>
<td>0.556</td>
<td>0.649</td>
<td>0.708</td>
<td>0.865</td>
<td>0.865</td>
<td>0.973</td>
</tr>
<tr>
<td>2550</td>
<td>0.157</td>
<td>0.253</td>
<td>0.357</td>
<td>0.461</td>
<td>0.560</td>
<td>0.654</td>
<td>0.713</td>
<td>0.784</td>
<td>0.872</td>
<td>0.980</td>
</tr>
<tr>
<td>2700</td>
<td>0.158</td>
<td>0.255</td>
<td>0.359</td>
<td>0.465</td>
<td>0.564</td>
<td>0.658</td>
<td>0.718</td>
<td>0.790</td>
<td>0.878</td>
<td>0.988</td>
</tr>
<tr>
<td>2850</td>
<td>0.159</td>
<td>0.249</td>
<td>0.346</td>
<td>0.442</td>
<td>0.530</td>
<td>0.663</td>
<td>0.723</td>
<td>0.796</td>
<td>0.884</td>
<td>0.994</td>
</tr>
<tr>
<td>3000</td>
<td>0.160</td>
<td>0.250</td>
<td>0.348</td>
<td>0.445</td>
<td>0.534</td>
<td>0.616</td>
<td>0.728</td>
<td>0.801</td>
<td>0.890</td>
<td>1.001</td>
</tr>
<tr>
<td>3150</td>
<td>0.161</td>
<td>0.252</td>
<td>0.350</td>
<td>0.448</td>
<td>0.537</td>
<td>0.620</td>
<td>0.732</td>
<td>0.806</td>
<td>0.895</td>
<td>1.007</td>
</tr>
<tr>
<td>3300</td>
<td>0.162</td>
<td>0.253</td>
<td>0.352</td>
<td>0.450</td>
<td>0.540</td>
<td>0.623</td>
<td>0.737</td>
<td>0.810</td>
<td>0.900</td>
<td>1.013</td>
</tr>
<tr>
<td>3450</td>
<td>0.163</td>
<td>0.247</td>
<td>0.354</td>
<td>0.453</td>
<td>0.543</td>
<td>0.627</td>
<td>0.741</td>
<td>0.815</td>
<td>0.905</td>
<td>1.018</td>
</tr>
<tr>
<td>3600</td>
<td>0.164</td>
<td>0.248</td>
<td>0.356</td>
<td>0.455</td>
<td>0.546</td>
<td>0.630</td>
<td>0.744</td>
<td>0.819</td>
<td>0.910</td>
<td>1.024</td>
</tr>
<tr>
<td>True Z</td>
<td>0.100</td>
<td>0.200</td>
<td>0.300</td>
<td>0.400</td>
<td>0.500</td>
<td>0.600</td>
<td>0.700</td>
<td>0.800</td>
<td>0.900</td>
<td>1.000</td>
</tr>
<tr>
<td>Average Z</td>
<td>0.157</td>
<td>0.258</td>
<td>0.361</td>
<td>0.460</td>
<td>0.551</td>
<td>0.640</td>
<td>0.733</td>
<td>0.823</td>
<td>0.915</td>
<td>0.996</td>
</tr>
<tr>
<td>std dev</td>
<td>0.009</td>
<td>0.011</td>
<td>0.011</td>
<td>0.013</td>
<td>0.013</td>
<td>0.018</td>
<td>0.020</td>
<td>0.027</td>
<td>0.037</td>
<td>0.036</td>
</tr>
<tr>
<td>CV%</td>
<td>5.47</td>
<td>4.41</td>
<td>3.01</td>
<td>2.82</td>
<td>2.44</td>
<td>2.75</td>
<td>2.77</td>
<td>3.25</td>
<td>4.07</td>
<td>3.58</td>
</tr>
<tr>
<td>Rel Bias%</td>
<td>56.70</td>
<td>29.09</td>
<td>20.25</td>
<td>14.90</td>
<td>10.29</td>
<td>6.59</td>
<td>4.68</td>
<td>2.92</td>
<td>1.65</td>
<td>-0.43</td>
</tr>
</tbody>
</table>
Table 5. Estimated Z based on a 1% detection criterion and maximum age observed

<table>
<thead>
<tr>
<th>sample size</th>
<th>Z</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.1</td>
<td>0.2</td>
<td>0.3</td>
<td>0.4</td>
<td>0.5</td>
<td>0.6</td>
<td>0.7</td>
<td>0.8</td>
<td>0.9</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>150</td>
<td>0.1706</td>
<td>0.2709</td>
<td>0.3542</td>
<td>0.4605</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.6579</td>
<td>0.7675</td>
<td>0.9210</td>
<td>0.9210</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>300</td>
<td>0.1354</td>
<td>0.2303</td>
<td>0.3070</td>
<td>0.3838</td>
<td>0.4605</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.6579</td>
<td>0.6579</td>
<td>0.7675</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>450</td>
<td>0.1212</td>
<td>0.2002</td>
<td>0.2878</td>
<td>0.3542</td>
<td>0.4187</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.6579</td>
<td>0.6579</td>
<td>0.7675</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>600</td>
<td>0.1123</td>
<td>0.1919</td>
<td>0.2709</td>
<td>0.3289</td>
<td>0.4187</td>
<td>0.4605</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.5756</td>
<td>0.6579</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>750</td>
<td>0.1071</td>
<td>0.1842</td>
<td>0.2558</td>
<td>0.3289</td>
<td>0.3838</td>
<td>0.4605</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.6579</td>
<td>0.6579</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>900</td>
<td>0.1023</td>
<td>0.1771</td>
<td>0.2424</td>
<td>0.3070</td>
<td>0.3838</td>
<td>0.4187</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.5756</td>
<td>0.6579</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1050</td>
<td>0.0980</td>
<td>0.1706</td>
<td>0.2424</td>
<td>0.3070</td>
<td>0.3542</td>
<td>0.4187</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.5756</td>
<td>0.6579</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1200</td>
<td>0.0959</td>
<td>0.1706</td>
<td>0.2303</td>
<td>0.3070</td>
<td>0.3542</td>
<td>0.4187</td>
<td>0.4605</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.5756</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1350</td>
<td>0.0940</td>
<td>0.1645</td>
<td>0.2303</td>
<td>0.2878</td>
<td>0.3542</td>
<td>0.4187</td>
<td>0.4605</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.5756</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1500</td>
<td>0.0921</td>
<td>0.1588</td>
<td>0.2303</td>
<td>0.2878</td>
<td>0.3542</td>
<td>0.4187</td>
<td>0.4605</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.5756</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1650</td>
<td>0.0921</td>
<td>0.1588</td>
<td>0.2193</td>
<td>0.2878</td>
<td>0.3542</td>
<td>0.3838</td>
<td>0.4605</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.5756</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1800</td>
<td>0.0921</td>
<td>0.1588</td>
<td>0.2193</td>
<td>0.2878</td>
<td>0.3289</td>
<td>0.3838</td>
<td>0.4605</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.5756</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1950</td>
<td>0.0921</td>
<td>0.1535</td>
<td>0.2193</td>
<td>0.2709</td>
<td>0.3289</td>
<td>0.3838</td>
<td>0.4605</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.5756</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2100</td>
<td>0.0921</td>
<td>0.1535</td>
<td>0.2193</td>
<td>0.2709</td>
<td>0.3289</td>
<td>0.3838</td>
<td>0.3838</td>
<td>0.4605</td>
<td>0.5117</td>
<td>0.5756</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2250</td>
<td>0.0921</td>
<td>0.1486</td>
<td>0.2093</td>
<td>0.2709</td>
<td>0.3289</td>
<td>0.3838</td>
<td>0.4187</td>
<td>0.5117</td>
<td>0.5756</td>
<td>0.5756</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2400</td>
<td>0.0921</td>
<td>0.1486</td>
<td>0.2093</td>
<td>0.2709</td>
<td>0.3289</td>
<td>0.3838</td>
<td>0.4187</td>
<td>0.5117</td>
<td>0.5117</td>
<td>0.5756</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2550</td>
<td>0.0921</td>
<td>0.1486</td>
<td>0.2093</td>
<td>0.2709</td>
<td>0.3289</td>
<td>0.3838</td>
<td>0.4187</td>
<td>0.4605</td>
<td>0.5117</td>
<td>0.5756</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2700</td>
<td>0.0921</td>
<td>0.1486</td>
<td>0.2093</td>
<td>0.2709</td>
<td>0.3289</td>
<td>0.3838</td>
<td>0.3838</td>
<td>0.4187</td>
<td>0.4605</td>
<td>0.5117</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2850</td>
<td>0.0921</td>
<td>0.1439</td>
<td>0.2002</td>
<td>0.2558</td>
<td>0.3070</td>
<td>0.3838</td>
<td>0.4187</td>
<td>0.4605</td>
<td>0.4605</td>
<td>0.5117</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3000</td>
<td>0.0921</td>
<td>0.1439</td>
<td>0.2002</td>
<td>0.2558</td>
<td>0.3070</td>
<td>0.3542</td>
<td>0.4187</td>
<td>0.4605</td>
<td>0.4605</td>
<td>0.5117</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3150</td>
<td>0.0921</td>
<td>0.1439</td>
<td>0.2002</td>
<td>0.2558</td>
<td>0.3070</td>
<td>0.3542</td>
<td>0.4187</td>
<td>0.4605</td>
<td>0.4605</td>
<td>0.5117</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3300</td>
<td>0.0921</td>
<td>0.1439</td>
<td>0.2002</td>
<td>0.2558</td>
<td>0.3070</td>
<td>0.3542</td>
<td>0.4187</td>
<td>0.4605</td>
<td>0.4605</td>
<td>0.5117</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3450</td>
<td>0.0921</td>
<td>0.1396</td>
<td>0.2002</td>
<td>0.2558</td>
<td>0.3070</td>
<td>0.3542</td>
<td>0.4187</td>
<td>0.4605</td>
<td>0.4605</td>
<td>0.5117</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3600</td>
<td>0.0921</td>
<td>0.1396</td>
<td>0.2002</td>
<td>0.2558</td>
<td>0.3070</td>
<td>0.3542</td>
<td>0.4187</td>
<td>0.4605</td>
<td>0.4605</td>
<td>0.5117</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

True Z       0.1000 | 0.2000 | 0.3000 | 0.4000 | 0.5000 | 0.6000 | 0.7000 | 0.8000 | 0.9000 | 1.0000 |
average Z    0.1008 | 0.1664 | 0.2320 | 0.2954 | 0.3539 | 0.4099 | 0.4694 | 0.5281 | 0.5878 | 0.6380 |
std dev      0.0185 | 0.0313 | 0.0389 | 0.0486 | 0.0527 | 0.0572 | 0.0631 | 0.0777 | 0.0970 | 0.0894 |
Rel Bias%    0.77 | -16.82 | -22.68 | -26.15 | -29.23 | -31.68 | -32.98 | -34.69 | -34.69 | -36.20 |
Table 6. Comparison of catch curve estimates based on truncated series with maximum age estimates for detection limits of 0.01 and 0.03. Max age is based on probability of occurrence of \(<1/n\) where \(n\) is the effective sample size. Effective sample size in this illustration is 100.

<table>
<thead>
<tr>
<th>Max Age in sample</th>
<th>True Z</th>
<th>Catch curve (Z) of frequencies, truncated to max age in sample</th>
<th>Catch curve (Z) based on rounded integer counts</th>
<th>Z estimate based on detection (1/n) threshold detection limit</th>
<th>Z estimate based on detection threshold = .03</th>
</tr>
</thead>
<tbody>
<tr>
<td>23</td>
<td>0.1</td>
<td>0.1</td>
<td>0.101</td>
<td>0.2002</td>
<td>0.1525</td>
</tr>
<tr>
<td>15</td>
<td>0.2</td>
<td>0.2</td>
<td>0.201</td>
<td>0.3070</td>
<td>0.2338</td>
</tr>
<tr>
<td>11</td>
<td>0.3</td>
<td>0.3</td>
<td>0.297</td>
<td>0.4187</td>
<td>0.3188</td>
</tr>
<tr>
<td>9</td>
<td>0.4</td>
<td>0.400</td>
<td>0.393</td>
<td>0.5117</td>
<td>0.3896</td>
</tr>
<tr>
<td>8</td>
<td>0.5</td>
<td>0.500</td>
<td>0.516</td>
<td>0.5756</td>
<td>0.4383</td>
</tr>
<tr>
<td>7</td>
<td>0.6</td>
<td>0.6</td>
<td>0.632</td>
<td>0.6579</td>
<td>0.5009</td>
</tr>
<tr>
<td>6</td>
<td>0.7</td>
<td>0.7</td>
<td>0.705</td>
<td>0.7675</td>
<td>0.5844</td>
</tr>
<tr>
<td>6</td>
<td>0.8</td>
<td>0.8</td>
<td>0.810</td>
<td>0.7675</td>
<td>0.5844</td>
</tr>
<tr>
<td>5</td>
<td>0.9</td>
<td>0.9</td>
<td>0.915</td>
<td>0.9210</td>
<td>0.7013</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>1.000</td>
<td>1.034</td>
<td>0.9210</td>
<td>0.7013</td>
</tr>
</tbody>
</table>
Figure 1. Log of probability density function for proportions at age for a population undergoing simple exponential decay due to the force of mortality Z.

Log PDF for Numbers at Age based on simple exponential model. Max age = 50 assumed.

Figure 1. Log of probability density function for proportions at age for a population undergoing simple exponential decay due to the force of mortality Z.
Figure 2. Expected maximum age in a sample of size $n$ under different levels of total mortality. Maximum true age = 50 years.