Piecewise Exponential Survivor Function, Intrinsic Rate of Growth and Stable Population for Blue Whales (*Balaenoptera Musculus)*: A Case Study[1]

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Abstract: This study delves into blue whale population dynamics and demographic modeling, emphasizing the repercussions of historical industrial hunting and the subsequent population decline. Employing continuous demographic models, we calculate intrinsic growth rates, construct life tables, and formulate stable population models. The research underscores the immense significance of blue whales, Earth's largest inhabitants, and emphasizes the drastic reduction in their population due to extensive commercial whaling during the 20th century. Using the piecewise exponential survivor function, a fitting tool for demographic modeling, we derive crucial demographic parameters and compare various models. Our findings underscore the precision and appropriateness of the piecewise exponential model, particularly in predicting demographic parameters for blue whale populations. Projections based on this model illuminate the slow recovery of the blue whale population, emphasizing the enduring impact of past exploitation.

Furthermore, we elaborate on our research approach, employing specific biological models as condensed case studies to captivate students and elucidate continuous demographic models during lectures on demography and life table analysis at the Department of Statistics, Technical University of Dortmund. It is essential to clarify that while our specialization lies in statistics and demography, our expertise is primarily centered within these domains rather than biology.

The analysis is founded on the piecewise exponential survivor function, proving to be a fitting choice for demographic modeling of blue whale populations, especially when data on mortality is limited and the primary objective does not involve analyzing the distribution of old age or estimating the maximum age. An advantageous feature of this simple function is its ability to yield fundamental formulas for key demographic parameters. Additionally, we illustrate our approach using the logistic function as a specific example, providing a tangible and insightful demonstration for our students.

1. Introduction

Continuous models of population dynamics are used to estimate the intrinsic growth rate and other demographic characteristics of blue whale populations. The basis of my investigation is an article by Branch (2008), who estimated with the Euler-Lotka equation the mean annual growth rate as 4.1%, using a simple survival function. He chose a stochastic model. For each of the input parameters, he assumed biologically plausible distributions: adult survival, calf survival, annual pregnancy rate, age at first parturition, and the proportion of births that are female. In my article, I adopt the variables and data from Branch (2008). However, I restrict myself to a deterministic representation. The approach of Branch (2008) is extended by considering alternative life tables and by calculating additional parameters. The focus is on a simple life table model, which has also been used implicitly by Branch: the piecewise exponential distribution. With the help of this distribution, we can derive simple formulas for the calculation of important demographic parameters.

Blue whales (*Balaenoptera musculus*) are the largest animals that have ever lived on earth. They can grow to a length of over 30 m and weigh 200 tons. At the beginning of the 20th century, their number was estimated between 250,000 and 300,000. Industrial hunting led to a massive collapse of their populations. In the 1970s and 1980s, there were bans and moratoriums on commercial whaling. These bans seem to have had some effect as the number

[1] An abbreviated version of this work was presented at the Arctic Observing Summit (AOS) 2022, held in Tromsø, Norway from March 30 to April 1, 2022.

of blue whales has increased from 5,000 (low point) in the 1990s to about 10,000 in 2010[2]. This doubling in the considered 20 years corresponds to a growth rate of about 3.5% per year. Blue whales are currently classified as endangered by the IUCN (International Union for the Conservation of Nature). Branch (2008a) estimated that the pre-exploitation abundance of the Antarctic blue whale was 256,000[3] (95% confidence interval 235,000-307,000). "*The rapid decline in the population to less than 1% of pre-exploitation abundance was the result of whaling mortality far exceeding maximum sustainable levels in all years from 1926/27 to 1971/72 except during World War II*" (Branch 2008a, p. 4). He continues: "*At the minimum point, the abundance was 0.15% of pre-exploitation levels (95% interval 0.1%-0.28%). The ratio of the abundance in 1997/98 (2280) to pre-exploitation abundance was 0.9% (95% interval 0.7%-1.0%).*"

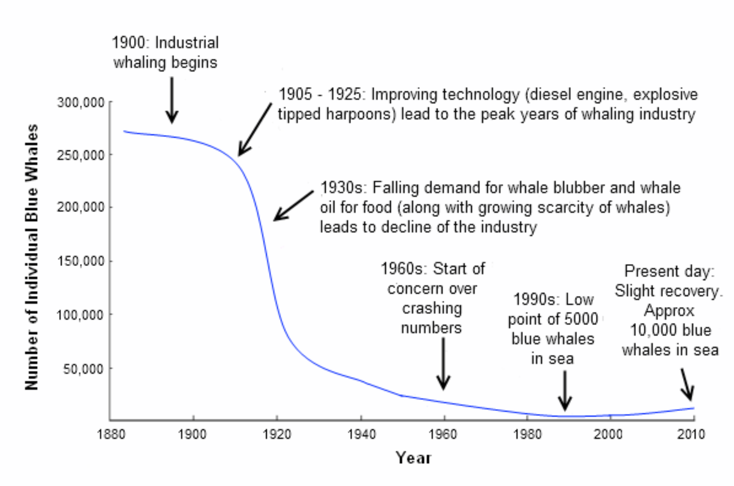

Fig. 1: Abundance of Antarctic blue whales
Source: https://britishseafishing.co.uk/what-is-the-largest-animal-in-the-sea/

2. Analysis using the piecewise exponential survivor function

2.1 Formulas for the life table

Notation and parameter values

S_1	first year survival rate	(S_1=0.84)
k	constant force of mortality	(k=0.037)
α	age of first parturition	(α=10)
m	constant maternity rate	(m=0.1971; cf. the calculation in section 2.2)
x	age	
r	(intrinsic) growth rate	(r=0.041; cf. the calculation in section 2.2)

Having reviewed the literature by Branch (2008) and specifically selecting values pertinent to whales, the chosen data for constructing the life table is as follows: The mean survival rate estimate for the first year, denoted as S_1, is 0.84. For whales aged one year or older, an assumed mean hazard rate or force of mortality (k) is set at 0.037, resulting in an approximate survival rate (S) of 0.963. However, the precise value is calculated as exp(-0.037) = 0.9637,

[2] For details, see, e.g., https://britishseafishing.co.uk/what-is-the-largest-animal-in-the-sea/ or https://iwc.int/blue-whale (International Whaling Commission)
[3] See also the logistic model in appendix I.

given the survival probability function formula p(x) = l(x+1)/l(x) = exp(-k) ~ 1 - k. Based on the chosen values, the piecewise exponential survivor function is derived as follows[4]:

$$l(x) = \begin{cases} l_1(x) = \exp(\ln S_1 \cdot x) = S_1^x & 0 \le x \le 1 \\ l_2(x) = S_1 \cdot \exp\left(-k \cdot (x-1)\right) & x > 1 \end{cases}$$

From the survival function, we derive the following functions and demographic parameters[5]:

Force of mortality function

$$\mu(x) = \begin{cases} \mu_1 = -\ln S_1 & 0 \le x \le 1 \\ \mu_2 = k & x > 1 \end{cases}$$

The force of mortality or hazard rate is defined by:

$$\mu(x) = -\frac{\frac{d\,l(x)}{d\,x}}{l(x)} = -\frac{d\,l(x)}{dx \cdot l(x)} = -\frac{d \ln l(x)}{dx}.$$

$\mu(x) \cdot dx$ is approximately the probability of dying between x and x+dx under the condition of not having died between 0 and x.

Knowing the force of mortality as a function of age, the survival function is got by integration as:

$$l(x) = e^{-\int_0^x \mu(z)dz}.$$

Death density function

$$f(x) = \begin{cases} -\ln S_1 \cdot \exp(\ln S_1 \cdot x) = S_1^x \cdot \ln S_1 & 0 \le x \le 1 \\ k \cdot S_1 \cdot \exp\left(-k \cdot (x-1)\right) & x \ge 1 \end{cases}$$

Life expectancy at birth

$$e(0) = \int_0^1 l_1(x)dx + \int_1^\infty l_2(x)dx = \frac{S_1 - 1}{\ln S_1} + \frac{S_1}{k}$$ (see also appendix II)

By linear interpolation of the function between 0 and 1, we get the approximation formula

$$e(0) \approx \frac{1+S_1}{2} + \frac{S_1}{k}.$$

[4] See also appendix II for a piece wise exponential survivor function: $H_1 = 0.17435 \cdot x = -\ln 0.84 \cdot x \quad 0 \le x \le 1$; $H_2 = 0.17435 + 0.037 \cdot (x-1) \quad x > 1$; $l_1(x) = \exp(-H_1)$; $l_2(x) = \exp(-H_2)$

[5] For an excellent introduction to life table analysis and continuous demographic models, see Keyfitz (1977).

Median age

$$x_{0.5} = 1 + \frac{\ln(2 \cdot S_1)}{k} \quad S_1 > 0.5$$

Keyfitz entropy

$$H = -\frac{\int_0^\infty l(x) \ln l(x) dx}{\int_0^\infty l(x) dx} = -\frac{\frac{S_1 \cdot \ln S_1}{k} + \frac{1 - S_1}{\ln S_1} - \frac{S_1}{k} + S_1}{\frac{S_1 - 1}{\ln S_1} + \frac{S_1}{k}}$$

Maximum age

$$x_{\max} = 1 - \frac{\ln\left(\frac{1}{N \cdot S_1}\right)}{k} = 1 + \frac{\ln(N \cdot S_1)}{k}$$

The maximum age has been estimated as the age of the last and only survivor of a population of size N, following a proposal of Gumbel (1937) and Finch and Pike (1996).

2.2 Formulas for the stable population model

After determining the life table, it is possible to formulate a population model for the blue whales. We use the continuous stable model, which is well known in demography. Only an overview of the stable theory in demography is given here. Detailed explanations and interpretations of the parameters are found elsewhere, e.g., Keyfitz (1968, 1977).

A population with an invariable age structure and a fixed rate of increase is called a stable population. The stable age structure is given by:

$$c(x)dx = e^{-rx} \cdot l(x)dx .$$

The stable intrinsic growth rate r can be determined by solving the characteristic equation:

$$1 = \varphi(r) = \int_\alpha^\beta e^{-rx} l(x) m(x) dx ,$$

where m(x) is the maternity function and $l(x)m(x)$ is the net maternity function. The limits of the integral are the youngest fertile age α and the highest β. The function $\varphi(r)$ crosses the vertical axis at the net reproduction rate

$$\varphi(0) = \int_\alpha^\beta l(x) m(x) dx = R_0 .$$

The extent to which women of given age x, on average, contribute to the births of future generations is expressed by Fisher's reproductive value:

$$\nu(x) = \frac{1}{e^{-rx} l(x)} \int_x^\beta e^{-ra} l(a) m(a) da .$$

The formulas for important parameters of the stable population with the growth rate r ($r \geq 0$) are:

Stable birth rate

$$b = \frac{\exp(r)\cdot(k+r)\cdot(r-\ln S_1)}{\exp(r)\cdot(k+r)-S_1\cdot(\ln S_1+k)}$$

Remark:

$$\frac{1}{b} = \int_0^1 e^{-rx}\cdot l_1(x)dx + \int_1^\infty e^{-rx}\cdot l_2(x)dx = \frac{S_1\cdot e^{-r}-1}{\ln S_1 - r} + \frac{S_1\cdot e^{-r}}{k+r}$$

Mean age of the stable population (approximation)

$$\mu_r = \frac{\int_0^{\inf} e^{-rx}\cdot x\cdot l(x)dx}{\int_0^{\inf} e^{-rx}\cdot l(x)dx} \approx \frac{1}{k+r}$$

Stable death rate

$$d = b - r$$

Fraction of the population aged x to x+dx

$$c(x)dx = \frac{\exp(-r\cdot x)\cdot l(x)}{\int_0^\infty \exp(-r\cdot x)\cdot l(x)}dx = \begin{cases} b\cdot\exp(-r\cdot x)\cdot\exp(\ln S_1)\cdot xdx & 0\leq x\leq 1 \\ b\cdot\exp(-r\cdot x)\cdot S_1\cdot\exp\left(-k\cdot\left(x-1\right)\right)dx & x\geq 1 \end{cases}$$

In particular:

$$\int_0^1 b\cdot\exp(-r\cdot x)\cdot\exp(\ln S_1)\cdot xdx = \frac{b\cdot e^{-r}\left(e^{-r}-S_1\right)}{r-\ln S_1}$$

$$\int_x^\infty b\cdot\exp(-r\cdot u)\cdot S_1\cdot\exp\left(-k\cdot\left(u-1\right)\right)du = \frac{b\cdot S_1\cdot e^{k-x\cdot(k+r)}}{k+r}$$

$$\int_1^\infty b\cdot\exp(-r\cdot x)\cdot S_1\cdot\exp\left(-k\cdot\left(x-1\right)\right)dx = \frac{b\cdot S_1\cdot e^{-r}}{k+r}$$

Median age of the stable population

$$x_{0.5}(r) = \frac{k-\ln\left(\frac{k+r}{2\cdot b\cdot S_1}\right)}{k+r}$$

The median follows from: $\dfrac{b \cdot S_1 \cdot e^{k-x\cdot(k+r)}}{k+r} = 0.5 \qquad S_1 > 0.5$

Characteristic function for the intrinsic growth rate

$$\Phi(r) = \int_{\alpha}^{\infty} e^{-rx} \cdot l(x) \cdot m(x)\, dx = \frac{m \cdot S_1 \exp\left(k \cdot (1-\alpha) - r \cdot \alpha\right)}{k+r}$$

Remark: with upper limit β

$$\Phi(r) = \int_{\alpha}^{\beta} e^{-rx} \cdot l(x) \cdot m(x)\, dx =$$

$$= \frac{m \cdot S_1 \exp\left(-k \cdot (\alpha + \beta - 1) - \beta \cdot r - \alpha \cdot r\right) \cdot \left(\exp\left(k \cdot \beta + \beta \cdot r\right) - \exp\left(k \cdot \alpha + \alpha \cdot r\right)\right)}{k+r}$$

Net reproduction rate

$$R_0 = \int_{\alpha}^{\infty} l(x) \cdot m(x)\, dx = \frac{m \cdot S_1 \exp\left(k \cdot (1-\alpha)\right)}{k}$$

Lotka-Euler equation (continuous version)

$$1 = \int_{\alpha}^{\infty} e^{-rx} \cdot l(x) \cdot m(x)\, dx = \frac{m \cdot S_1 \exp\left(k \cdot (1-\alpha) - r \cdot \alpha\right)}{k+r}$$

The equation cannot be explicitly solved for the intrinsic growth rate r. Therefore, only a numerical solution is possible, e.g., iterative methods (Newton-Raphson method; Regula Falsi).

An approximation by a Taylor series of order 2 leads to the following quadratic equation:

$$\left(\alpha \cdot e^{(k \cdot u)} \cdot (k \cdot \alpha + 2)\right) \cdot r^2 + \left(2 \cdot e^{(k \cdot \alpha)} \cdot (k \cdot \alpha + 1)\right) \cdot r + \left(2 \cdot k \cdot e^{(k \cdot \alpha)} - 2 \cdot m \cdot S_1 \cdot e^{k}\right) = 0$$

Mean of net maternity function

$$A_0 = \frac{\int_{\alpha}^{\inf} x \cdot l(x) \cdot m(x)\, dx}{\int_{\alpha}^{\inf} l(x) \cdot m(x)\, dx} = \frac{\int_{\alpha}^{\inf} x \cdot l(x) \cdot m(x)\, dx}{R_0} = \frac{1}{k} + \alpha$$

Mean age at birth

$$A_r = \frac{\int_{\alpha}^{\beta} x \cdot e^{-rx} \cdot l(x) \cdot m(x)\, dx}{\int_{\alpha}^{\beta} e^{-rx} \cdot l(x) \cdot m(x)\, dx} = \frac{1 + \alpha \cdot (k+r)}{k+r}$$

Lotka interval

$$T_r \approx \frac{A_0 + A_r}{2}$$

This parameter is an indicator of the mean generation time.

With $R_0 \approx e^{T_r \cdot r}$ follows an approximation formula for the intrinsic rate of growth, if the mean generation time is known:

$$r \approx \frac{1}{T_r} \cdot \ln R_0 .$$

Reproductive value

$$\nu(x) = \begin{cases} \int_\alpha^\beta e^{-ra} \cdot l(a) \cdot m(a)\, da = 1 & x = 0 \\ \frac{1}{e^{-rx} \cdot l(x)} \cdot \int_\alpha^\beta e^{-ra} \cdot l(a) \cdot m(a)\, da = \frac{1}{e^{-rx} \cdot l(x)} = \frac{\exp(k+r) \cdot x - k}{s} & 1 \le x < \alpha \\ \frac{1}{l(x)} \cdot \int_x^\beta e^{-r(a-x)} \cdot l(a) \cdot m(a)\, da = \frac{1}{e^{-rx} \cdot l(x)} \cdot \int_x^\beta e^{-ra} \cdot l(a) \cdot m(a)\, da = \frac{m}{k+r} & x \ge \alpha \end{cases}$$

2.3 Numerical results and graphs

Figure 2 illustrates the survivor function and the force of mortality function. Important life table parameters are given in Table 1.

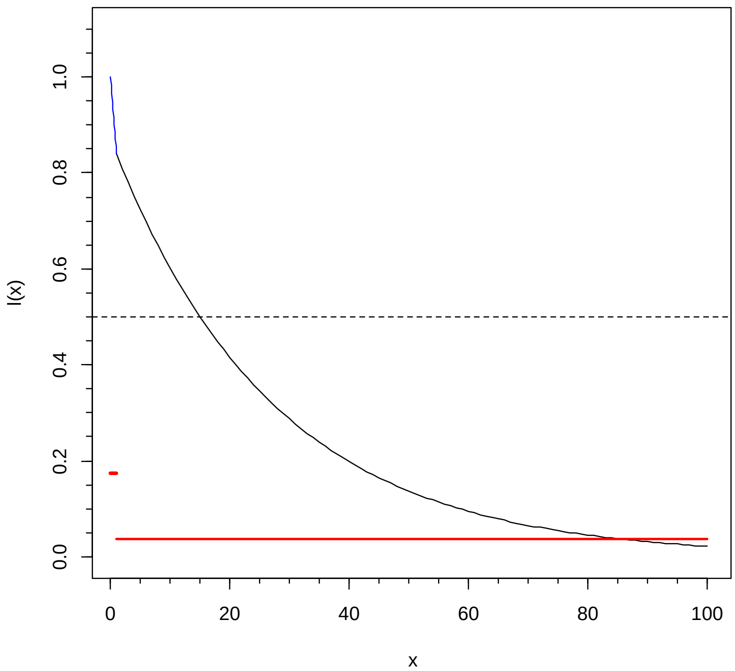

Fig. 2: Piecewise survivor function and force of mortality function (red) (S_1=0.84, $\mu_1 = -\ln(0.84) = 0.174 \quad 0 \le x \le 1$, $\mu_2 = k = 0.037 \quad x > 1$)

Table 1: Important parameters of the life table

Parameter	Value
Life expectancy at birth	23.6
Median age	15
Keyfitz entropy H	1.13
Maximum age (N=100)	120.8
Maximum age (N=1000)	183

The Keyfitz entropy is a measure of the rectangularization of the life table. H becomes smaller when the survivor function moves to a rectangular form. H=0, if all mortality is concentrated at one age. The entropy of H=1.13 is greater than the entropy of the exponential distribution with H=1, where the force of mortality is the same at all ages.

Since the force of mortality does not increase with age, unrealistically high maximum ages are obtained. The maximum age of blue whales is reported as 110 years[6].

Branch (2008) takes as annual pregnancy rate an interval which is between 1/3 and 1/2. The arithmetic mean is $5/12 \approx 0.4167$. If we take into account the proportion of births that are female, 0.473, we finally arrive at a constant maternity rate of 0.1971. First, we calculate the intrinsic rate of growth from the Euler-Lotka equation. We get

$$1 = \frac{0.1971 \cdot 0.84 \cdot \exp\left(0.037 \cdot (1-10) - r \cdot 10\right)}{0.037 + r}$$

The numerical solution yields the intrinsic growth rate r = 0.0414.

(Approximative) solutions of the resulting quadratic equation

$$34.31 \cdot r^2 + 3.97 \cdot r - 0.2365 = 0$$

are $r_1 =$ 0.0433 and $r_2 =$ -0.159.

The actual growth rate depends on fertility, mortality, and age structure. It will deviate from the intrinsic one if the age structure is not stable. Here, the actual growth rate will fluctuate around the true one with decreasing oscillations and will eventually approach the intrinsic one. The oscillations can be considerable and the time of adjustment can be long (see, e.g., Pflaumer, 2013), especially if the population size is small and the age structure is very unstable at the beginning. A discrete projection model (Leslie-matrix) is needed to illustrate the trajectory of the actual growth rate.

[6] https://genomics.senescence.info/species/entry.php?species=Balaenoptera_musculus

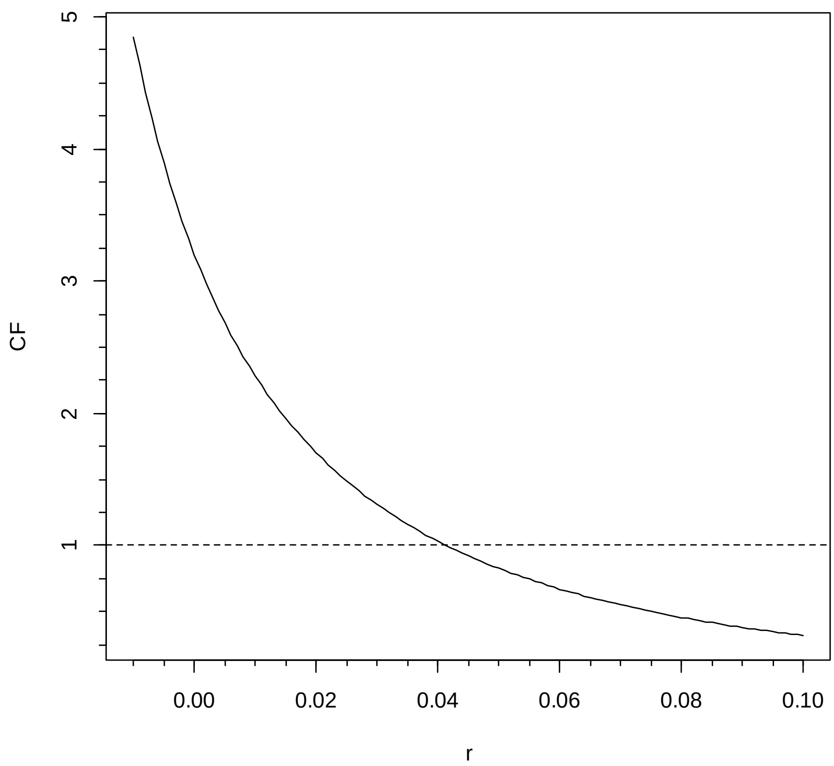

Fig. 3: Characteristic function

The assumption of infinity for the upper bound of the maternity function has only a minor influence on the value of the intrinsic rate of growth, as calculations in Table 2 show. Therefore, the simplified formula is sufficient.

Table 2: Influence of the upper limit β

Upper limit of β	r
40	0.0363
50	0.0393
75	0.0411
100	0.0414
Inf.	0.0414

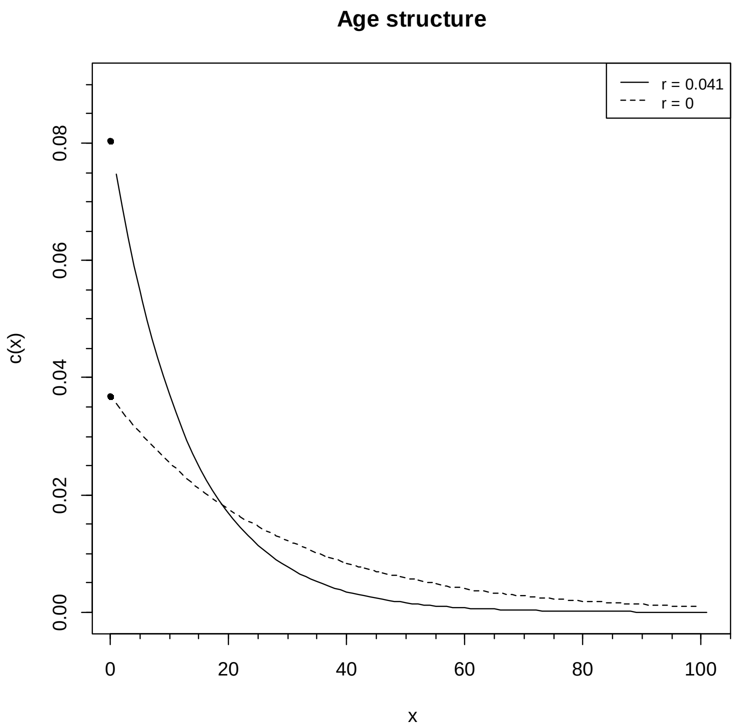

Fig. 4: Age distribution of the stable population (b=0.08944, r=0.0414, k=0.037, S_1=0.84)

Table 3: Age distribution of the stable population

age	proportion
0-1	0.0804
>1	0.9196

age > x	10	20	30	40	50	60	70	80	90	100
proportion	0.4541	0.2074	0.0947	0.0432	0.0197	0.009	0.0041	0.0019	0.0009	0.0004

Note that, e.g., the proportion over 60 years is less than 1 percent, although the survival function has no upper bound.

Table 4: Relevant parameters of the stable population

Parameter	**Value**
Intrinsic rate of growth r	0.0414
Stable birth rate b	0.0894
Stable death rate d	0.0481
Net reproduction rate R_0	3.21
Mean age of the stable population $\mu(r)$	12.76
Median age of the stable population	8.77
A_0	37.03
A_r	22.76
T_r	29.89

Table 5: Reproductive values

x	0	1	2	3	4	5	6	7	8	9	10	>10
ν(x)	1.00	1.24	1.34	1.45	1.57	1.70	1.84	1.99	2.15	2.32	2.51	2.51

The reproductive value is constant for ages 10 years and older (see Table 5). Harvesting or culling adult blue whales influences population size in the stable population, that is 2.5 times greater than harvesting or culling newborn offspring.

3. Life table extensions

3.1 A three-parameter model

One criticism of the previous approach is that the force of mortality function is not continuous. A continuous force of mortality function can be represented by:

$\mu(x) = B \cdot e^{-g \cdot x} + k$ with $\mu(0) = B + k$.

The corresponding survivor function is given by:

$$l(x) = \exp\left(\frac{B}{g} \cdot e^{-gx} - k \cdot x - \frac{B}{g}\right) = \exp\left(\frac{B}{g} \cdot e^{-gx}\right) \cdot \exp\left(-k \cdot x - \frac{B}{g}\right)$$

with the parameters B>0,g>0 and k>0.

If we assume that the growth rate g is high, such that $e^{-gx} \approx 0$, then and we can approximate the survivor function after a certain age x by:

$$l(x) = \exp\left(-k \cdot x - \frac{B}{g}\right) = \exp\left(-\frac{B}{g}\right) \cdot \exp(-k \cdot x) \qquad x > x_0$$

The following relationship exists between B and g

$$B = \frac{g \cdot e^{g} \cdot (\ln(S_1) + k)}{1 - e^{g}},$$

provided that $l(1) = S_1$.

We cannot solve explicitly the equation for g.

Given S_1, it is easier to specify B as g, since we know that $\mu(0) \approx B$. One should remember that $\mu(x) \cdot dx$ is approximately the probability of dying between x and x+dx. If we (arbitrarily) assume that 2.5% of newborns die in the first month, then $B \cdot \frac{1}{12} \approx 0.025$ or $B \approx 0.3$. With this value of B, g can then be determined from the above equation.

Example: k=0.037, S_1=0.84, B=0.3, g=1.84; $\exp\left(-\frac{B}{g}\right) = 0.8496$

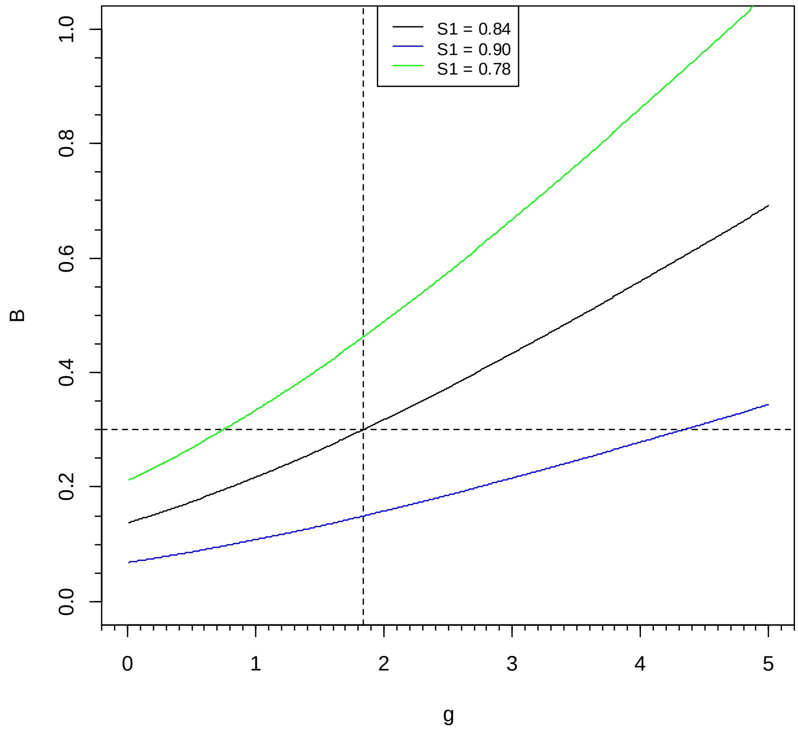

Fig. 5: Combinations of g and B, which yield the same S_1

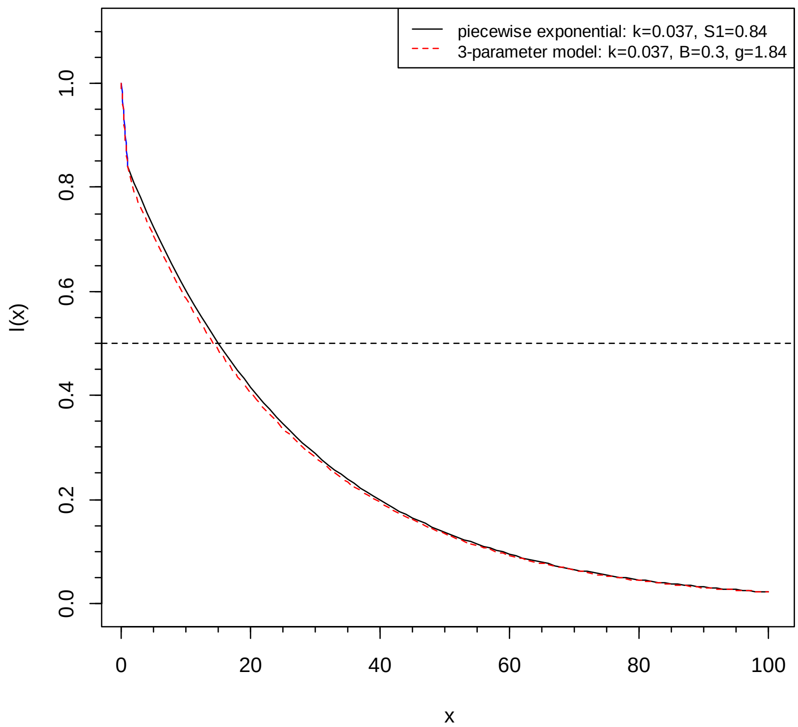

Fig. 6: Comparison of the life tables

Table 6: Important parameters of the life tables

Parameter	Piecewise exponential	3-parameter model
Life expectancy at birth	23.6	23.04
Median age	15	14.33
Keyfitz entropy H	1.13	1.156
Maximum age (N=100)	120.8	120.1
Maximum age (N=1000)	183	182.3

We get here the intrinsic growth rate r=0.0403, if using the Lotka-Euler equation with the values of the example:

$$1 = \int_{\alpha}^{\infty} m \cdot \exp(-r \cdot x) \exp\left(\frac{B}{g} \cdot e^{-gx} - k \cdot x - \frac{B}{g} \right) dx .$$

Both life table models lead to almost identical results for the age structure and the demographic parameters, as the growth rates hardly differ. Parameters and age structures have to be determined by numerical integration (see detailed results in Table 7 and Table 8). No relevant formulas exist for the three-parameter model, except for the maximum age:

$$x_{\max} = \frac{\ln(N)}{k} - \frac{B}{g \cdot k} .$$

We get almost the same maximum ages 120.06 (N=100) and 182.29 (N=1000) as before.

Table 7: Comparison: Age distribution of the stable populations

	piecewise exponential	3-parameter model
age	proportion	proportion
0-1	0.0804	0.0797
>1	0.9196	0.9203

age>x	proportion	proportion
10	0.4541	0.4585
20	0.2074	0.2117
30	0.0947	0.0977
40	0.0432	0.0451
50	0.0197	0.0208
60	0.0090	0.0096
70	0.0041	0.0044
80	0.0019	0.0020
90	0.0009	0.0009
100	0.0004	0.0004

Table 8: Comparison: Demographic parameters of the stable populations

	piecewise exponential	3-parameter model
Parameter	**Value**	**Value**
Intrinsic rate of growth r	0.0414	0.0403
Stable birth rate b	0.0894	0.0904
Stable death rate d	0.0481	0.051
Net reproduction rate R_0	3.21	3.13
Mean age of the stable population $\mu(r)$	12.76	12.85
Median age of the stable population	8.77	8.88
A_0	37.03	37.03
A_r	22.76	22.94
T_r	29.89	29.98

3.2 A four-parameter model

The models considered so far resulted in implausible maximum ages. Non-increasing force of mortality from high ages is the reason. The following function shows a decreasing pattern for young ages and an increasing pattern for old ages:

$$\mu(x) = B \cdot e^{-g \cdot x} + A \cdot e^{q \cdot x} \qquad \text{with } \mu(0) = B + A.$$

This force of mortality function is based on a mortality formula of the famous mathematician Carl Friedrich Gauß (1777-1855) (see, e.g., Loewy, 1906 or Pflaumer, 2013). Adding a constant hazard leads to a five-parameter model with three components, first proposed by Lazarus (1867) and later by Siler (1979). The distribution and its properties are described in Pflaumer (2015, p. 2666 f.). Siler applies the model to animal mortality.

Integration of the four-parameter hazard rate $\mu(x)$ leads to the survivor function

$$l(x) = \exp\left(\frac{A}{q} - \frac{B}{g} - \frac{A}{q} \cdot e^{qx} + \frac{B}{g} \cdot e^{-gx}\right).$$

If we assume that the growth rate g is high, such that $e^{-gx} \approx 0$, then we can approximate the survivor function after a certain age x by:

$$l(x) = \exp\left(\frac{A}{k} - \frac{B}{g} - \frac{A}{k} \cdot e^{qx}\right) = e^{-\frac{B}{g}} \cdot \exp\left(\frac{A}{k} - \frac{A}{k} \cdot e^{qx}\right) = e^{-\frac{B}{g}} \cdot l_{Go}(x) \quad x > x_0,$$

where $l_{Go}(x)$ is the survivor function of the Gompertz distribution.

Example: A=0.037; q=0.005; B=0.3; g=1.84

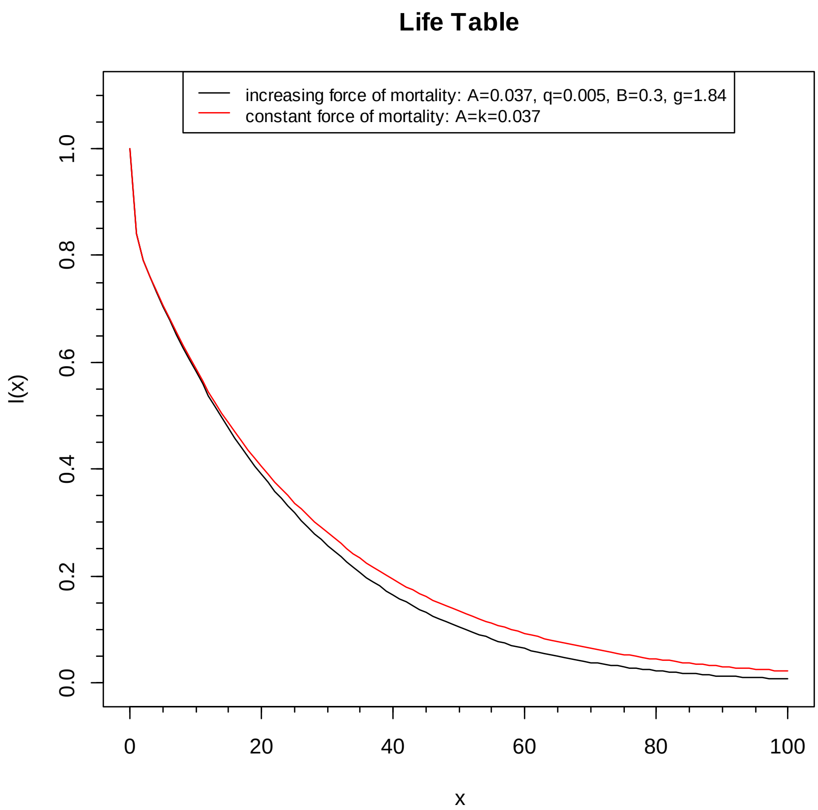

Fig. 7: Comparison of life tables: Constant versus increasing force of mortality

The life expectancy of the five-parameter model in Figure 7 decreases to 20.5 years because of the increasing force of mortality at old ages. The Euler-Lotka equation leads to a lower intrinsic rate of growth of r=0.0374. However, the initial growth rate of r=0.0413 could be achieved if the constant term of the increasing hazard rate were reduced from A=0.037 to A=0.03365.

A formula can be derived for the maximum age

$$x_{\max} = \frac{\ln\left(\frac{g \cdot q \cdot \ln N + A \cdot g - B \cdot q}{A \cdot g}\right)}{q}$$

In our example, the maximum ages are 94 (with N=100) and 129.6 (with N=1000) respectively.

4. Conclusions

The utilization of the piecewise exponential survival function emerges as a judicious choice for modeling the demographic dynamics of blue whale populations, particularly in situations where comprehensive data on mortality is scarce. This approach is especially valuable when the primary objective does not encompass analyzing the intricacies of old age distribution or estimating the maximum age of the population. A notable advantage of employing this straightforward function is its ability to yield fundamental formulas for critical demographic parameters. Furthermore, survival functions incorporating continuous hazard functions tend to yield comparable results. However, they necessitate the estimation of supplementary parameters, a task that can be impractical, especially considering the constraints posed by limited data available for wild cetacean populations.

In summary, the piecewise exponential survival function stands as a pragmatic and effective tool for studying blue whale demographics, allowing for meaningful insights and predictions within the constraints of available data and research objectives. Its simplicity and ability to derive essential demographic parameters make it a valuable asset in the field of population dynamics, facilitating a deeper understanding of blue whale populations and aiding in their conservation efforts.

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Appendix

I. A dynamic logistic model for Antarctic blue whales

Following Branch (2008a, p. 3), the pre-exploitation abundance of Antarctic blue whales is estimated using the logistic function (a S-shaped curve). It is arbitrarily assumed that the minimum abundance is 1,000 in 1970.

The model is:

$$N_{1905} = K$$
$$N_{t+1} = N_t + r \cdot N_t \cdot \left(1 - \frac{N_t}{K}\right) - C_t,$$

where K is the carrying capacity (maximum value of the curve), assumed equal to pre-exploitation abundance, and C_t is the catch in year t. The annual catches are given in Table 1. The growth rate r is assumed to be 4.1% yearly.

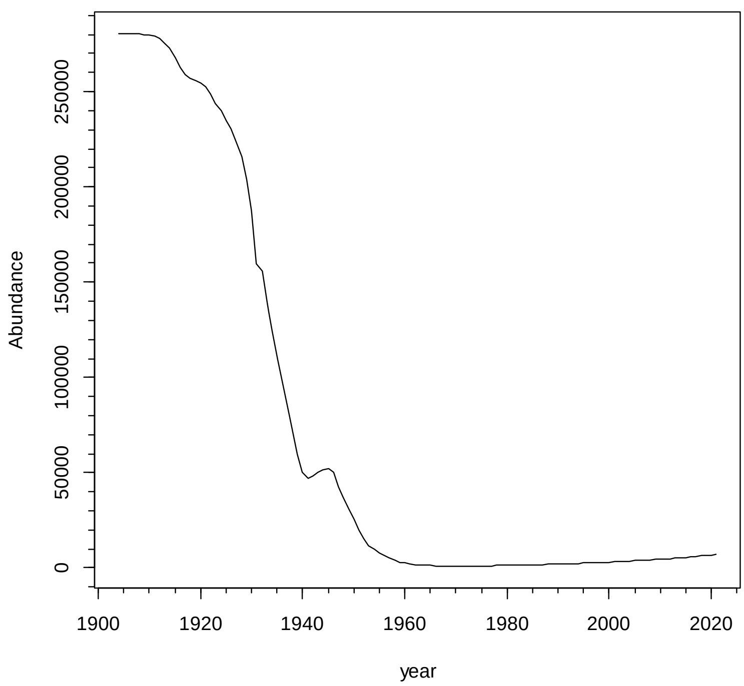

Figure 1: Estimated abundance of Antarctic blue whales

The estimated pre-exploitation abundance (K) was 280,471 in 1904. The population trend in Figure 1 shows a steady and sharp decline, interrupted only by the Second World War. From 1970, the population grew from the assumed minimum of 1000 to about 7150 in 2021. Growth rates, yearly population changes, and catches are illustrated in Figures 2 and 3.

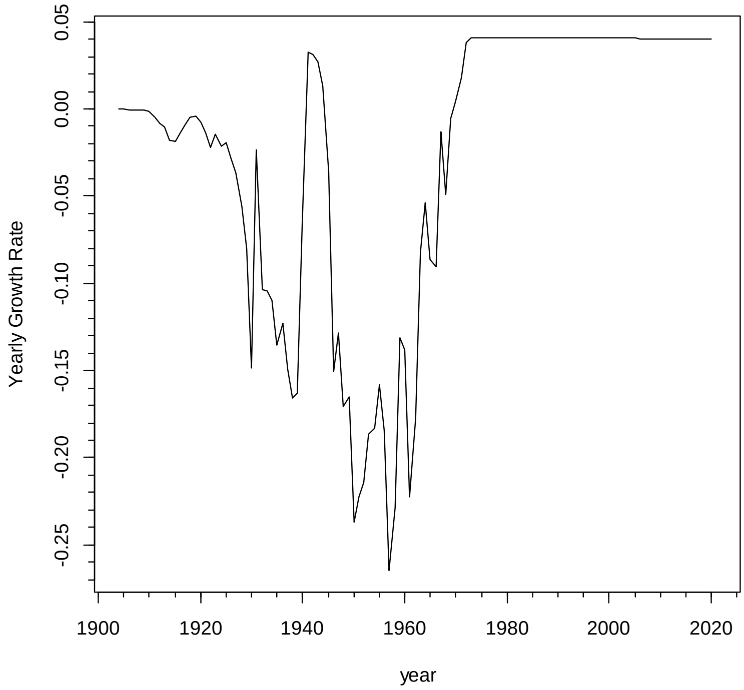

Figure 2: Estimated yearly growth rates of Antarctic blue whales

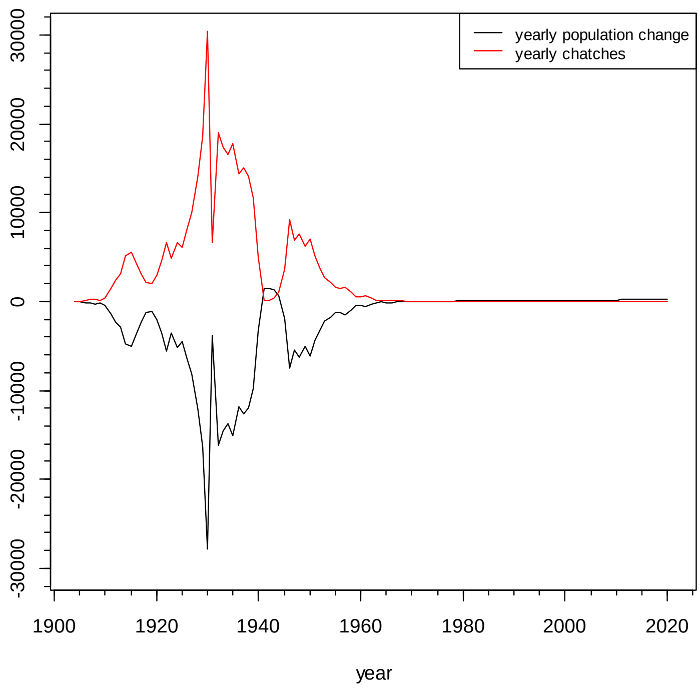

Figure 3: Estimated yearly population changes and yearly catches of Antarctic blue whales (see also Table 1)

We will use again the logistic model to forecast the population. Figure 4 shows the population trajectory. At current estimated rates, it will take nearly 140 years for the population to recover to even half its pre-exploitation abundance. A recently accepted estimate of Antarctic blue whale abundance south of 60°S from three complete circumpolar surveys is from Branch (2007), who gives the number as 2,280 whales in 1997/98. The above model in Figure 1 predicts the abundance to be 2,800 in 1998.

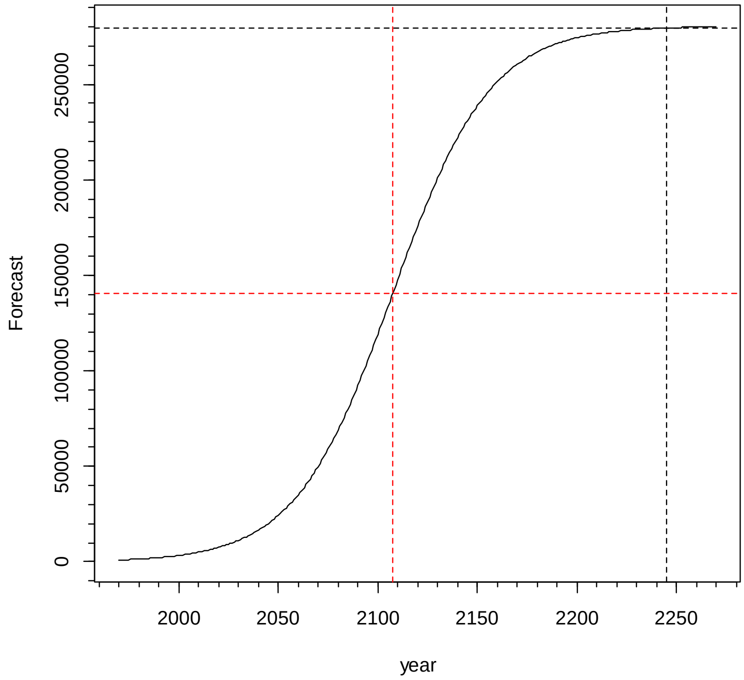

Figure 4: Population projection of Antarctic blue whales (assuming 1970: 1000)

Forecast Model:

$$N_t = \frac{K}{1 + b \cdot e^{-r \cdot t}} = \frac{280{,}471}{1 + 279{,}471 \cdot e^{-0.041 \cdot t}} \quad t = 0,1,2... \quad (1970, 1971, ...)$$

$$b = \frac{K}{N_0} - 1 \rightarrow b = \frac{280{,}471}{1{,}000} - 1 = 279{,}471$$

$t_{K/2} = \frac{\ln b}{r}$; time until half saturation level is reached: $t_{140235.5} = 137.4$ (years) or in 2107

$t_{K-N_0} = 2 \cdot \frac{\ln b}{r}$; time until the population size is saturation level minus N_0:

$t_{280{,}471-1000} = 274.8$ (years) or in 2245

Table 1: Annual catches of Antarctic blue whales

year	catches	*year*	catches	*year*	catches	*year*	catches
1904	11	*1922*	6694	*1940*	4973	*1958*	1082
1905	51	*1923*	4829	*1941*	63	*1959*	534
1906	111	*1924*	6629	*1942*	126	*1960*	481
1907	201	*1925*	6028	*1943*	346	*1961*	611
1908	244	*1926*	8143	*1944*	1047	*1962*	395
1909	176	*1927*	10006	*1945*	3603	*1963*	183
1910	422	*1928*	14130	*1946*	9234	*1964*	129
1911	1477	*1929*	18608	*1947*	6936	*1965*	164
1912	2391	*1930*	30365	*1948*	7641	*1966*	155
1913	3113	*1931*	6577	*1949*	6196	*1967*	58
1914	5125	*1932*	18961	*1950*	7057	*1968*	95
1915	5503	*1933*	17413	*1951*	5111	*1969*	47
1916	4356	*1934*	16578	*1952*	3851	*1970*	37
1917	3061	*1935*	17815	*1953*	2704	*1971*	23
1918	2143	*1936*	14414	*1954*	2171	*1972*	3
1919	1987	*1937*	15019	*1955*	1578		
1920	2955	*1938*	14110	*1956*	1504		
1921	4552	*1939*	11722	*1957*	1667		

Source: Branch (2008a, p. 6)

II. Example of a piecewise exponential survivor function with 3 constant hazard functions

Hazard rate or force of mortality:

$$\mu(x) = \begin{cases} h_1 & 0 \le x \le x_1 \\ h_2 & x_1 < x \le x_2 \\ h_3 & x > x_2 \end{cases}$$

Cumulated hazard rates:

$$H(x) = \begin{cases} H_1 = h_1 \cdot x & 0 \le x \le x_1 \\ H_2 = h_1 \cdot x_1 + h_2 \cdot (x - x_1) & x_1 < x \le x_2 \\ H_3 = h_1 \cdot x_1 + h_2 \cdot (x_2 - x_1) + h_3 \cdot (x - x_2) & x > x_2 \end{cases}$$

Survival function:

$$l(x) = \begin{cases} e^{-H_1} & 0 \le x \le x_1 \\ e^{-H_2} & x_1 < x \le x_2 \\ e^{-H_3} & x > x_2 \end{cases}$$

Remarks: $l_i(x) = e^{-H_i}$; death density function: $f_i(x) = l(x) \cdot h_i$ has jump discontinuities at x_i.

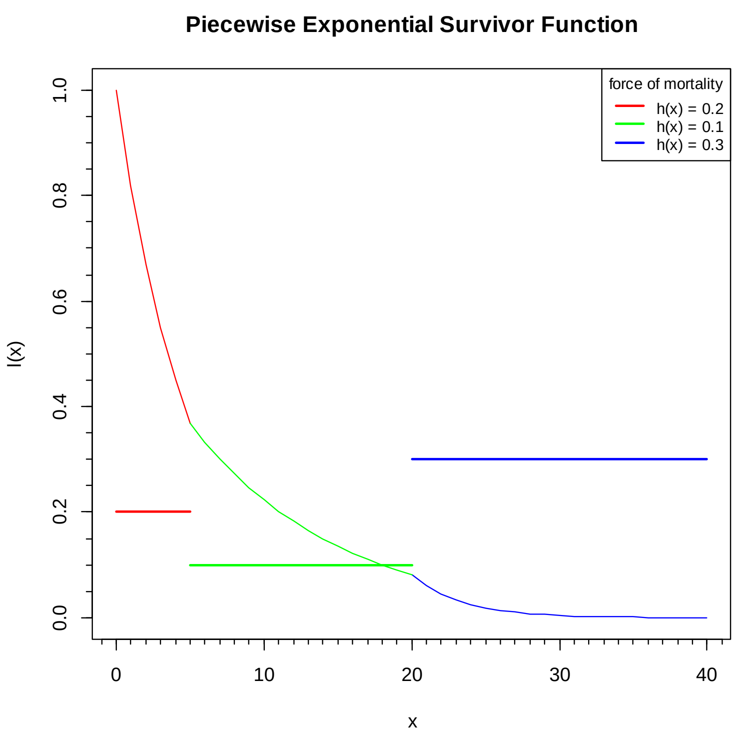

Figure 5: Piecewise exponential survivor function (x_1=5; x_2=20)

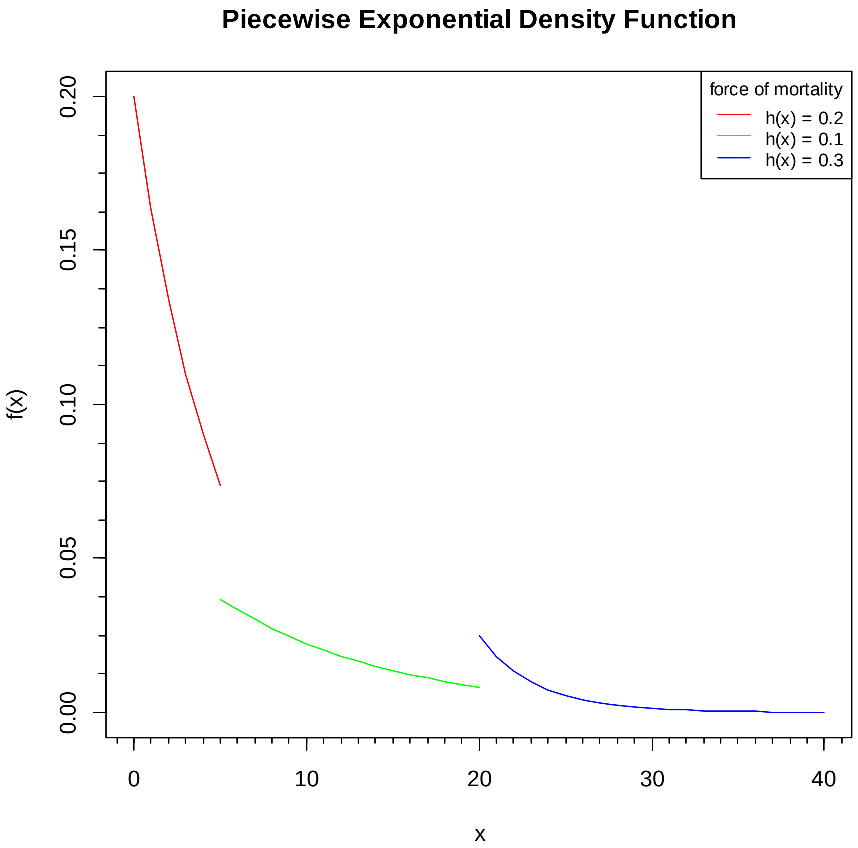

Figure 6: Piecewise exponential density function (x_1=5; x_2=20)

Life expectancy:

3 pieces:

$$e(0) = \int_0^{x_1} \exp\left(-h_1 \cdot x\right) dx + \int_{x_1}^{x_2} \exp\left(-h_2 \cdot x\right) dx + \int_{x_2}^{\infty} \exp\left(-h_3 \cdot x\right) dx$$

$$= \frac{1}{h_1} + \exp(-h_1 \cdot x_1) \cdot \left(\frac{1}{h_2} - \frac{1}{h_1} + \exp\left(-h_2 \cdot (x_2 - x_1)\right) \cdot \left(\frac{1}{h_3} - \frac{1}{h_2} \right) \right)$$

$$e(0) = \frac{1}{h} \quad if \;\; h_1 = h_2 = h_3 = h$$

Example: $x_1 = 5;\ x_2 = 20;\ h_1 = 0.2;\ \ h_2 = 0.1;\ h_3 = 0.3 \ \rightarrow \ e(0) = 6.29$

2 pieces:

$$e(0) = \int_0^{x_1} \exp\left(-h_1 \cdot x\right) dx + \int_{x_1}^{\infty} \exp\left(-h_2 \cdot x\right) dx = \frac{1}{h_1} + \exp(-h_1 \cdot x_1) \cdot \left(\frac{1}{h_2} - \frac{1}{h_1} \right)$$

Example: $x_1 = 1;\ h_1 = 0.174;\ h_2 = 0.037 \rightarrow e(0) = 23.63$

$$\text{e}(0) \begin{cases} = \dfrac{1}{\mu_1} & \text{if} \quad \mu_1 = \mu_2 \\ > \dfrac{1}{\mu_1} & \text{if} \quad \mu_1 > \mu_2 \\ < \dfrac{1}{\mu_1} & \text{if} \quad \mu_1 < \mu_2 \end{cases}$$