Modelling harvesting animal population at constant rate and constant effort

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Abstract**—**Harvesting animal population at constant rate and effort is presented, solved and modelled in this article. The governing equations are solved analytically. Survival conditions are found and limiting cases are shown. Excel implementations of the solution are presented. Harvesting the world populations of the Sperm whale and American bison are modelled and analyzed.

Keywords**—**harvesting model, animal population, extinction

I. Introduction

THE problem of harvesting animal population is topical. Many animal species became extinct by human activity long time ago, e.g. bears in the UK [1], but some have become extinct worldwide just recently, e.g. western black rhinoceroses [2]. There are species that were saved at the last moment, e.g. the American bison [3] and most of the whale species in 1986 when commercial whaling was banned. However, there are many species threatened by extinction, yet still hunted or caught, e.g. more than 40 species of fish in the Mediterranean Sea could disappear in few years [4], [5]. Mathematical models illustrate well how overhunting causes species to become extinct after some time while judicious approach to harvesting enables them to survive.

The problems of harvesting animal population at constant rate and constant effort are governed by differential equations derived from the famous logistic function, which is the limiting case if there is no harvest [6], [7], [8]. General solutions are e.g. in [9] and [10]. Analysis of the equilibriumis in [7], [8], [11].

This article gives the complete analytically solutions to harvesting animal population at constant rate and constant effort in sections 2 and 6. The conditions for surviving the species are found, being the crucial points of the solutions. The solution is discussed and the limiting cases are shown in sections 3 and 7. Excel implementations of the solutions are presented in sections 4 and 8. Harvesting the world population of the Sperm whale (Physetermacrocephalus) at constant rate is modelled and analyzed in section 5. Harvesting the world population of the American bison (Bison bison) at constant effort is modelled and analyzed in section 9.

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II. Harvesting animal population at constant rate

The problem of harvesting at constant rate is governed by the equation [6], [7]

$$\dot{x} = rx\left(1-\frac{x}{K}\right)-h\,,\ \ x(0)=x_0\,, \tag{1}$$

where $x(t)$ is the number of individuals at time $t \geq 0$, x_0 is the number at $t=0$, r is the growth rate, which is the change in the number per year and capita at unlimited supply of food, K is the carrying capacity, which is the maximum number that the territory can provide with food, and h is the harvesting rate, which is the number that is annually taken away. If $h=0$, then Eq. (1) reduces to the logistic growth equation. The steady state is given by the condition $\dot{x}=0$. If the equation $x=0$ has a positive root t_{ex}, then the species will become extinct at $t=t_{\text{ex}}$. Otherwise, the species will survive and the number will stabilize at $\lim\limits_{t\to\infty} x$.

It is clear from the following form of Eq. (1)

$$\dot{x} = -\frac{r}{K}\left(x-\frac{K}{2}\right)^2+\left(\frac{rK}{4}-h\right) \tag{2}$$

that the solution splits in three parts given by the conditions $h<rK/4$, $h=rK/4$, and $h>rK/4$.

1) If $h<rK/4$, then there are two steady states

$$K''=K\left(\frac{1}{2}-A\right),\ \ K'=K\left(\frac{1}{2}+A\right), \tag{3}$$

where

$$A=\sqrt{\frac{1}{4}-\frac{h}{rK}}\,. \tag{4}$$

The following five cases are possible:

1a) If $x\in(K'',K')$, then the solution to Eq. (2) is

$$x = \frac{K}{2} + KA\tanh\left(rAt + \operatorname{arctanh}\frac{X_0}{A}\right), \tag{5}$$

where

$$X_0 = \frac{x_0}{K} - \frac{1}{2}. \tag{6}$$

It is an ascending function. It holds that $\lim_{t\to\infty} x = K'$ The species will survive and x will stabilize at K' (Fig. 1 part II, Fig. 5a, Fig. 5b).

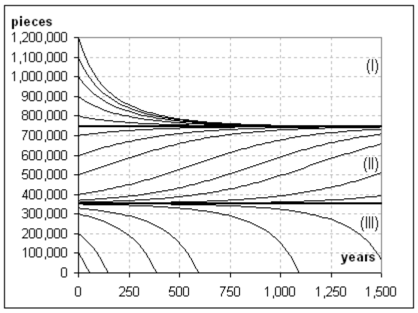

Figure 1 Solution to Eq. (2) if r = 0.01, K = 1,100,000, h = 2400, and x_0 = (from top to bottom, $\times 10^3$) 1200; 1100; 1000; 900; 800; 746.21 (bold line); 700; 600; 500; 400; 370; 360; 355; 354; 353.78 (bold line); 353; 350; 330; 300; 200; 100;

1b) If $x \in (0, K'') \cup (K', \infty)$ then the solution to Eq. (2) is

$$x = \frac{K}{2} + KA\coth\left(trA + \operatorname{arccoth}\frac{X_0}{A}\right). \tag{7}$$

It is a descending function. There are two alternatives:

1b1) If $x \in (K', \infty)$, then the species will survive and stabilize at K' (Fig. 1 part I, Fig. 6a).

1b2) If $x \in (0, K'')$, then equation $x = 0$ has the solution (Figs. 1 part III, 5d)

$$t_{\text{ex}} = \frac{1}{rA}\left(\operatorname{arccoth}\left(-\frac{X_0}{A}\right) - \operatorname{arccoth}\frac{1}{2A}\right). \tag{8}$$

1c) If $x = K''$ or $x = K'$, then the system is in a steady state, that is, $\dot{x} = 0$ thus x is constant.

1c1) If $x = K'$, then it follows from Eq. (2) that $\ddot{x} = -2rA < 0$, which means that the steady state is stable. If x_0 changes, the system returns to this state (upper bold line in Fig. 1).

1c2) If $x = K''$, then it follows from Eq. (2) that $\ddot{x} = 2rA > 0$. The steady state is unstable. If x_0 increases, the system will turn to the case $x \in (K'', K')$ and the species will survive. If x_0 decreases, then the system will turn to the case $x \in (0, K'')$ and the species will become extinct (lower bold line in Fig. 1, full line in Fig. 5c).

2) If $h = rK/4$, then it follows from Eq. (2) that x is descending. There is the steady-state $K' = K/2$. The solution to Eq. (2) is

$$x = \frac{K}{2} + \frac{KX_0}{1 + X_0 rt}. \tag{9}$$

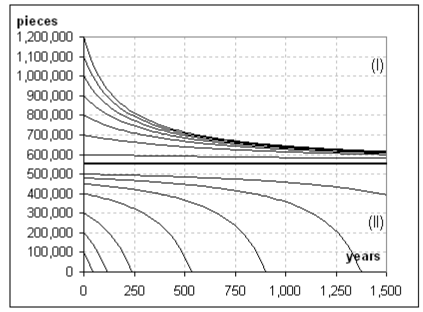

Figure 2 Solution to Eq. (2) if r = 0.01, K = 1,100,000, h = 2750, and x0 = (from top to bottom, $\times 10^3$) 1,200; 1,100; 1,000; 900; 800; 700; 600; 550; 500; 480; 450; 400; 300; 200; 100

2b) If $x < K/2$, then equation $x = 0$ has the solution (Figs. 2 part II, Fig. 5e)

$$t_{\text{ex}} = -2\frac{x_0}{K}\frac{1}{X_0 r}. \tag{10}$$

2c) If $x = K/2$, then $\dot{x} = 0$ thus x is constant. The system is in a steady state that is a merger of the two steady states from part 1c. If x_0 increases, then the species will survive, but if x_0 decreases, then the species will become extinct (Fig. 2, bold line).

3) If $h > rK/4$, then it follows from Eq. (2) that x is descending. There is no steady state. The solution to Eq. (2) is

$$x = \frac{K}{2} - KB\tan\left(rBt - \arctan\frac{X_0}{B}\right), \tag{11}$$

where

$$B = \sqrt{\frac{h}{rK} - \frac{1}{4}}. \tag{12}$$

Equation $x = 0$ has the solution (Fig. 3, Fig. 5f, Fig. 6c)

$$t_{\text{ex}} = \frac{1}{rB}\left(\arctan\frac{X_0}{B} + \arctan\frac{1}{2B}\right). \tag{13}$$

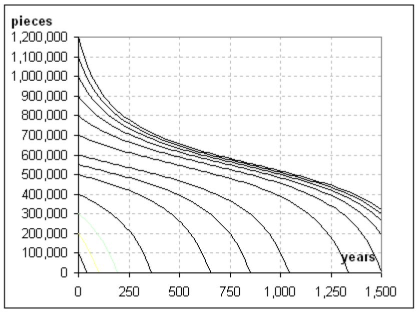

Figure 3 Solution to Eq. (2) if r = 0.01, K = 1,100,000, h = 3000, and x_0 = (from top to bottom, $\times 10^3$) 1,200; 1,100; 1,000; 900; 800; 700; 600; 550; 500; 400; 300; 200; 100

III. Discussions

Eq. (7) can be rearranged into the form

$$x = \frac{K}{2} + KA\frac{X_0 \coth(rAt) - A}{A\coth(rAt) + X_0}. \tag{14}$$

Then

$$\lim_{A\to 0} x = \frac{K}{2} + K\frac{X_0 \lim_{A\to 0}(A/\tanh(rAt))}{\lim_{A\to 0}(A/\tanh(rAt)) + X_0} = \frac{K}{2} + \frac{KX_0}{1 + X_0 rt}, \tag{15}$$

which is Eq. (9). Eq. (11) can be rearranged into the form

$$x = \frac{K}{2} + KB\frac{X_0 - B\tan(rBt)}{B + X_0 \tan(rBt)}. \tag{16}$$

Then

$$\lim_{B\to 0} x = \frac{K}{2} + \lim_{B\to 0}\frac{KX_0 - KB\tan(rBt)}{1 + X_0 \tan(rBt)/B} = \frac{K}{2} + \frac{KX_0}{1 + X_0 r t}, \tag{17}$$

which is Eq. (9) , again.
If $h \to 0$ and $x_0 < K$, then Eq. (5) reduces to

$$x = \frac{x_0(\tanh(rt/2) + 1)}{1 + \tanh(rt/2)(2x_0/K - 1)} = \frac{x_0 K}{x_0 + (K - x_0)\mathrm{e}^{-rt}}, \tag{18}$$

which is the logistic function.
If $h = 0$ and $x_0 > \mathrm{K}$, then Eq. (7) reduces to

$$x = \frac{x_0(\coth(rt/2) + 1)}{\coth(rt/2) + (2x_0/K)} = \frac{x_0 K}{x_0 + (K - x_0)\mathrm{e}^{-rt}}, \tag{19}$$

which is the logistic function, again.

IV. Excel implementation

The Excel implementation of the solution is in Fig. 4. Function IF is largely used due to the three parts of the solutions. Inputs r, K and x_0 are in range C2:C4. Input h is in cell F2. The time range is in cell F3. Parameters X_0 and $rK/4$ are calculated in range I2:I3. Parameter A and B are calculated in cells I4 and I5 provided $h < rK/4$ for A or $h > rK/4$ for B otherwise the cells are blank. The maximum harvesting to keep $x(t)$ ascending is calculated in cell L2 by the formula =C4*C2*(1-C4/C3). The extinction time is calculated in range N3:P3 separately for the parts 1, 2 and 3 of the solution provided it exists, otherwise the cells are blank. Cell L3 contains the formula =IF(P3<>"",P3,IF(N3<>"",N3,IF(O3<>"",O3,""))) that puts in the cell the extinction time from cells N3:P3 if there is any.

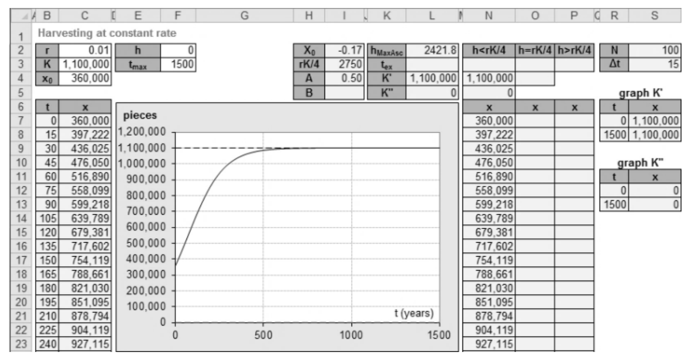

Figure 4 Excel application; Sperm whale harvesting if x_0 = 360,000 and h = 0

K' and K'' are calculated in cells N4, N5 and O4 provided they exist, otherwise the cells are blank. Cells L4 and L5 contain =IF(N4<>"",N4,IF(O4<>"",O4,"")) and =IF(N5<>"",N5,IF(O4<>"",O4,"")) that put in the cells the values of K' and K'' from cells N4, N5 and O4 if there are any. The time range is divided to 100 subintervals (cell S2). The step is calculated in cell S3. The graph is made over 101 points in range B7:C107. Cell B7 contains 0. Cell B8 contains =B7+$S$3, which is filled down as far as row107. The function values are calculated in range N7:P107 separately for each part of the solution or the cells are blank, subject to the conditions. Cell C7 contains =IF($F$2>$I$3,P7,IF($F$2<$I$3,N7,O7)), which puts in the cell the actual function value from range N7:P7. The formula is filled down as far as row107. The points that give the beginning and end of the dashed lines that depict K' and K'' are calculated in ranges R7:S8 and R12:S13.

V. Harvesting the Sperm whale population

According to the IUCN Red List [12], it holds for the Sperm whale that $r = 0.01$, $K = 1{,}100{,}000$, which is the estimated number of the species around year 1700 when commercial whaling started, $x_0 = 360{,}000$, which is the estimated number in year 1986 when commercial whaling ended. There is no harvesting in Fig. 4. That is the logistic growth model. Animal number x stabilizes at K after some time. The model shows that it will take 532 years from 1986 to reach 99 % of K. In Figs. 5a-5c, harvesting$h$ is small enough to enable the species to survive; number x stabilizes at $K' < K$. In Figs. 5d-5f, harvesting h is too large, and the species becomes extinct after some time. Figs. 5b and 5d show that the maximum harvesting to survive is $h = 2{,}421$ at $K' = 740{,}237$; as $h = 2{,}422$ causes the species to become extinct after 2,364 years.

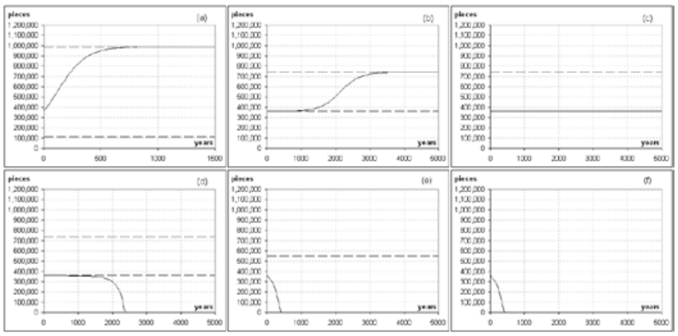

Figure 5 Sperm whale harvesting if x_0 = 360,000: a) h = 1,000, K' = 988,748; b) h = 2,421, K' = 740,237; c) h = 2,421.81 (unreal), K' = 360,000 = x_0; d) h = 2,422, t_{ex} = 2364; e) h = 2,750, t_{ex} = 379; f) h = 2,751, t_{ex} = 378

If the harvesting was 2,750 pieces a year, the species would become extinct after 379 years (Fig. 5e). If the harvesting was 2,751, it would become extinct after 378 years (Fig. 5e). If the harvesting was 5,000 pieces a year, it would vanish after 104 years. The modern highly mechanized phase of whaling was particularly intense around 1950 when around 25,000 sperm whales were killed per year, which dramatically decreased the population [12]. It can be shown by the model that the species would vanish after 15 years.

If the commercial whaling started now, then $x_0 = K = 1{,}100{,}000$. The case is shown in Fig. 6. If the harvesting was 2,700 pieces a year, the species would survive at $K' = 624{,}162$ (Fig.6a). The maximum harvesting that enables the species to survive is 2750 pieces a year at $K' = K/2 = 550{,}000$ (Fig. 6b) as 2751 would cause extinction after 32,549 years (Fig. 6c).

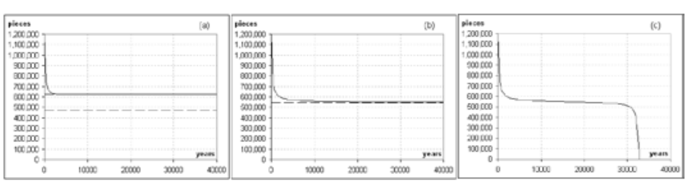

Figure 6 Sperm whale harvesting if x0 = 1,100,000:
a) h = 2,700, K' = 624,162; b) h = 2,750, K' = 550,000 = K/2;
c) h = 2,751, tex = 32,549

If the harvesting was 5,000 pieces a year, it would become extinct after 104 years. If the harvesting was 25,000, the species would become extinct after 48 years.

VI. Harvesting Animal Population at Constant Effort

The problem is governed by the equation [6], [7]

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1-\frac{x}{K}\right) - Ex\,, \quad x(0) = x_0\,, \tag{20}$$

where $E \geq 0$ is the harvesting effort, which is the number of individuals per capita that are annually taken away.

Let $E = br$. Eq. (20) takes the form

$$\dot{x} = rx\left(1-b-\frac{x}{K}\right), \quad x(0) = x_0\,. \tag{21}$$

Note that $x = 0$ is the trivial steady state.

The solution to Eq. (21) splits to three parts given by the conditions $b < 1$, $b = 1$ and $b > 1$.

1) If $b < 1$, then there is the steady state $x = (1-b)K = K'$.

Three are three cases possible:

1a) If $x \in (0, K')$, then the solution to Eq. (21) is (Fig. 7, lower half)

$$x = KA\left[1 + \tanh\left(rAt + \operatorname{arctanh}\frac{X_0}{A}\right)\right], \tag{22}$$

where $X_0 = \frac{x_0}{K} - A$ and $A = \frac{1-b}{2}$. It is an ascending function. It holds that $\lim_{t\to\infty} x = K'$.

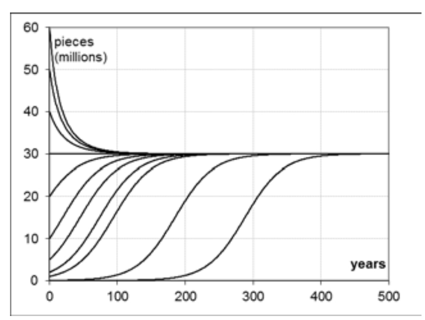

Figure 7 Solution to Equation (21) if r = 0.0716, K = 60 million and b = 0.5; K' = 30 million; right bottom to left top: x_0 = (thousands) 1; 40; (millions) 1; 2; 5; 10; 20; 30; 40; 50; 60

1b) If $x \in (K', \infty)$, then the solution to Eq. (21) is (Fig. 7, upper half)

$$x = KA\left[1 + \coth\left(rAt + \operatorname{arccoth}\frac{X_0}{A}\right)\right]. \tag{23}$$

It is a descending function. It holds that $\lim_{t\to\infty} x = K'$.

1c) If $x = K'$, then the system is in a steady state. It follows from Eq. (21) that $\ddot{x} = -r(1-b)$ at $x = K'$. The steady state is stable (note $b < 1$; the horizontal line in Fig. 7).

2) If $b = 1$, then the solution to Eq. (21) is

$$x = \frac{x_0 K}{K + x_0 rt}. \tag{24}$$

It is a descending function (Fig. 8). It holds that $\lim_{t\to\infty} x = 0$. The equation $x = 0$ has no solution but the species becomes practically extinct if $x = 1$. Equation $x = 1$ has the solution

$$t_{ex} = \frac{K}{r}\left(1 - \frac{1}{x_0}\right). \tag{25}$$

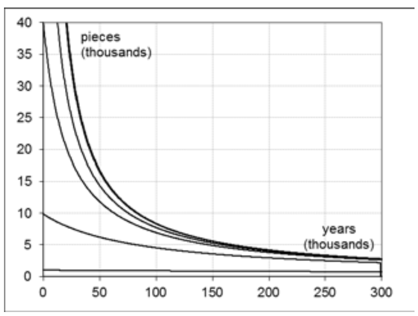

Figure 8 Solution to Eq. (21) if r = 0.0716, K = 60 million and b = 1; bottom to top: x_0 = (thousands) 1, 10, 40, 100, (millions, merged) 1, 60; t_{ex} between 599 and 600 million years

3) If $b > 1$, then the solution is given by Eq. (23) (Fig. 9). It holds that $\lim_{t\to\infty} x = 0$ as $A < 1$. Equation $x = 0$ has no solution. Equation $x = 1$ has the solution

$$t_{ex} = \frac{1}{rA}\left[\operatorname{arccoth}\left(\frac{1}{KA} - 1\right) - \operatorname{arccoth}\frac{X_0}{A}\right]. \tag{26}$$

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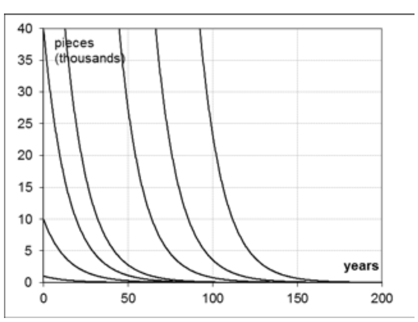

Figure 9 Solution to Eq. (21) if r = 0.0716, K = 60 million, b = 2; left bottom to right top: x_0 = (thousands) 1, 10, 40, 100, (millions) 1, 5, 60; t_{ex} = (years) 96, 129,148, 161, 193, 214, 240

VII. Discussions

Eq. (23) can be rearranged into the form

$$x = KA + KA\frac{X_0 \coth(rAt) - A}{A\coth(rAt) + X_0}. \tag{27}$$

Then

$$\lim_{A\to 0} x = K\frac{X_0 \lim_{A\to 0}(A/\tanh(rAt))}{\lim_{A\to 0}(A/\tanh(rAt)) + X_0} = \frac{KX_0}{1 + X_0 rt}, \tag{28}$$

which is Eq. (24). If $b \to 0$, that is, $A \to 1/2$, and $x < K$, then it holds for Eq. (22) that

$$\lim_{A\to 1} x = \frac{x_0(\tanh(rt/2) + 1)}{1 + \tanh(rt/2)(2x_0/K - 1)} = \frac{x_0 K}{x_0 + (K - x_0)e^{-rt}}, \tag{29}$$

which is the logistic function. If $b \to 0$ and $x > K$, then it holds for Eq. (23) that

$$x(t) = \frac{x_0(\coth(rt/2) + 1)}{\coth(rt/2) + (2x_0/K)} = \frac{x_0 K}{x_0 + (K - x_0)e^{-rt}}, \tag{30}$$

which is the logistic function, again.

VIII. Excel Implementation

The Excel implementation of the solution is in Fig. 10. Inputs r, K and x_0 are in range C2:C4. Input b is in cell F2. The time range is in cell F3.

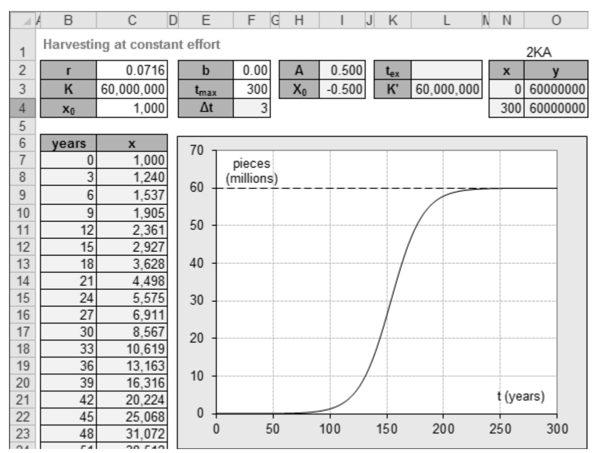

Figure 10 Excel application; American bison harvesting if r = 0.0716, K = 60 million, x_0 = 1,000 and b = 0

Parameters A and X_0 are calculated in range I2:I3. The extinction time is calculated in range L2 provided it exists otherwise the cell is blank. K' is calculated in cell L3 provided it exists otherwise the cell is blank. The time increment is calculated in cell S5 as one hundredth of the time range. The graph is made over 101 points in range B7:C107. Cell B9 contains 0. Cell B10 contains =B9+$S$5, which is filled down as far as row107. The function values are calculated in range C7:C107 subject to the conditions that hold for the solution.The points that give the beginning and end of the dashed line that depicts K' are in rangeN3:O4.

IX. Harvesting the American bison population

The estimated number of the American bison before year 1800 was about $K = 60{,}000{,}000$ [13]. The estimated number of remaining bison by the late 19th Century was about 1,000 [13]. The number of plains bison in 2010 was more than 20,500 in 62 conservation herds (the number under commercial propagation was about 400,000). The number of wood bison in 2008 was about 10,870 in 11 conservation herds [13]. The growth rate of American bison is $r = 0.0716$ [14](average of the growth rate of 21 bison herds).Figure 10 shows that if $x_0 = 1{,}000$ and there is no harvest, that is, $b = 0$, then the number reaches 99% of the carrying capacity 60 million in 218 years (Fig. 10). If $b = 0.5$, that is, the harvest is half of the population growth each year, then the number reaches 30 million in about 400 years (Fig. 7). If $x_0 = 60{,}000{,}000$ and $b = 1$, then the species will become extinct in about 600 million years (Fig. 8); if $b = 2$, then the species will become extinct in 240 years (Fig. 9); if $b = 2.5$ then the number drops to $x = 780$ in 100 years. That means that the number of killed pieces between years 1800 and 1900 was about twice and a half of the population growth each year.

X. Conclusions

The problem of harvesting animal population at constant rate and constant effort are solved analytically in this article. Excel implementations of the solutions are presented. Harvesting the world population of the Sperm whale at constant rate and the American bison at constant effort are modelled and analyzed. The first model shows that it will take 532 years for the Sperm whale to reach 99 % of the carrying capacity of 1,100,000 from the number of 360,000 in 1986, when commercial whaling was banned, if there is no harvest. The maximum harvest to survive is 2,421 pieces a year; the number stabilizes at 740,237 pieces, then. It the harvest was 2,422, the species would become extinct after 2,364 years. The second model shows that it would take 218 years for the American bison to reach 99 % of the carrying capacity of 60 million from the number of 1,000 in about year 1900, when conservation started, if there would be no harvest. The average harvesting ratebetween years 1800 and 1900, when the number dropped from 60 million to 780, wastwice and half the population growth.

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