Population Modeling with Exponential: Logistic Equation

Peter K. Anderson
Graham Supiri
Doris Benig

Abstract

The exponential function becomes more useful for modelling size and population growth when a braking term to account for density dependence and harvesting is added to form the logistic equation. Using these functions, models are developed to explain population growth, equilibrium and local species extinction for particular application in fisheries.

Key words: Exponential function, logistic equation, ordinary differential equation, integration, differentiation, invariant, fishery.

Introduction

This paper was developed in the context of the need for growth models in general but for sustainable fisheries in particular. To this end, the necessary mathematics needs to be developed and here the role of exponential function e^x is pivotal. This is a unique function because the derivative of the function is the same as the function or alternately we can state that the function is invariant under differentiation. Having this property makes it both unique among the known functions and also one of the most important functions in pure and applied mathematics.

This paper will derive the invariant property and illustrate its use in modelling, growth and decay of physical and biological situations. At the first level, an application of a linear first order Ordinary Differential Equation (ODE) will be made to model population growth, equilibrium, harvesting and extinction**.** We first define the exponential function and note its special properties.

Exponential Function

An exponential function has the form $f(x) = b^x$, where x is the exponent and b, a constant. A very useful form is obtained when b is replaced by $e \approx 2.71828\ldots$, a transcendental number (an infinite series of nonrepeating decimals). The function e^x is unique because the derivative of the function is the same as the function (Misra et al. 2017). We consider $f(x)$ to be a function such that:

$$df(x)/dx = f(x), \qquad (1)$$

which can be also presented (treating the derivative as a differential and cross multiplying) as:

$$1/f(x)\, df(x) = dx.$$

Integrating both sides with respect to their respective variables, we have:

$$\ln f(x) = x, \qquad (2)$$

which can be written equivalently as:

$$f(x) = e^x. \qquad (3)$$

Allowing for an arbitrary constant, c, in the right hand side of (3) after integration, we obtain a general solution function:

$$f(x) = e^{x+c} = e^x.\, e^c, \quad \text{or} \quad b.e^x,$$

where $b = e^c$ is a constant. This result (3) can also be obtained by considering e^x as defined by the power series expansion:

$$e^x = \sum_{n=\infty}^{\infty} \frac{x^n}{n!} = 1 + x + \frac{x^2}{2!} + \frac{x^3}{3!} + \ldots$$

or, alternately by:

$$e^x = \lim_{n\to\infty} \left(1 + \frac{x}{n}\right)^n.$$

Then, by taking derivatives of both sides of the equation, we have:

$$\frac{d}{dx}(e^x) = \frac{d}{dx}\left(1 + x + \frac{x^2}{2!} + \frac{x^3}{3!} + \ldots\right) = \left(0 + 1 + \frac{2x}{2!} + \frac{3x^2}{3!} + \ldots\right) =$$

$$\left(1 + x + \frac{x^2}{2!} + \ldots\right) = e^x$$

thereby confirming (3). Thus, we can conclude that the function e^x remains invariant under differentiation which, as previously noted, makes it one of the most important functions in pure and applied mathematics. This invariance property:

$$\frac{d\ e^x}{dx} = e^x,$$

whereby the rate of growth of the function equals the value of the function models many biological, mechanical and other systems. We can also note, more generally, that if $f(x) = c\, e^{kx}$ where c and k are arbitrary constants:

$$f'(x) = \frac{d(ce^{kx})}{d(kx)} \cdot \frac{d\ kx}{dx} \text{ (the chain rule)} = k\, c\, e^{kx} = k\, f(x). \quad (4)$$

Here c is an arbitrary constant making $f(x) = c\, e^{kx}$ a general solution to the ODE (1): $d f/dx = f$.

Other ways of expressing this property include: slope of the graph or the rate of increase of the function at x is the value of the function at x; the function $y = e^x$ solves the differential equation $y' = y$ or $\frac{dy}{dx} = y$; and variables such as growth or decay rates are proportional to size.

Since this property can be interpreted as the rate of growth at any point (e.g. in time) of the function being equal to the value of the function at that point, it can be used in first order linear differential equations (Zill, 2013, p84) to model many biological and other systems where individual or population growth (or decay) rate depends on the present state (e.g. size) of the system. To demonstrate the widespread usefulness of this exponential function, we now explore its application to population growth.

Exponential equations for population growth.

Here we introduce the use of the exponential function by considering a biological population that grows at a rate of 0.2, say, of its size with growth function given by:

$$y' = 0.2y$$

$$or\ \frac{dy}{dt} = 0.2 f(t)$$

which, from (4) and (2), will have the solution:

$y = c\,e^{0.2t}$ where k (in (4)) = 0.2.

Now note that if $y = a^x$ rather than e^x,

then $\ln_a y = x$ or $\dfrac{\ln_e y}{\ln_e a} = x$

giving $\ln_e y = x \ln_e a$ or $y = e^{x \ln_e a}$ (5)

and

$$\frac{dy}{dx} = e^{x \ln a} \ln a \,, \tag{6}$$

using the chain rule.

We now consider a population starting with a single individual ($y_0 = 1$) which doubles in size every 3 years and so is represented by:

$y = 2^{t/3} y_0$ and so $y = 2^{\frac{t}{3}}$, (7)

where t is the number of years of growth. This population growth function can be written in the form:

$y = e^{\frac{t}{3}\ln 2}$ from (5),

From which we derive $\dfrac{dy}{dt} = \dfrac{\ln 2}{3} e^{\frac{t}{3}\ln 2}$ = 0.231 $e^{0.231t}$. (8)

This can also be shown to be equivalent to:

$$\frac{dy}{dt} = 0.231 \text{x} 2^{\frac{t}{3}}$$

with $y = 2^{\frac{t}{3}} \quad = e^{\frac{t}{3}\ln 2}$ from (6)

$$\frac{dy}{dt} = \frac{\ln 2}{3} e^{\frac{t}{3}\ln 2} \quad = \frac{\ln 2}{3} 2^{\frac{t}{3}}.$$

From (4) above, we can note that $k = \ln 2/3$.

We can now consider an initial value problem with ODE growth function $y' = 3y$, with an initial value of $y(0) = 5.7$. This can be written in the form:

$$dy/dx = 3y.$$

From (4) above we have:

$$y = ce^{3x}, \text{ as a general solution}$$

and since y(0) = 5.7, ce^0 giving $c = 5.7$, we conclude $y = 5.7\, e^{3x}$, as the particular solution for initial conditions. We now proceed to apply these models to population growth.

Standard models for Population Growth

We consider a population of single celled organisms such as bacteria (Vandemeer, 2010) in an environment with unlimited food supply, and where individual cells divide once a day. We replace the continuous variable y with the discrete variable N to model population size in terms of numbers. Thus, from an initial population of N_0 and a population N_t after t days, the population size will be (from (7)):

$$N_t = 2^t N_0.$$

More generally, we can replace 2 by R and write:

$$N_t = R^t \; N_0 \tag{9}$$

where R is the *rate of population increase* (Figure 1).

It turns out to be very convenient in formulating models to express R as e^r, where r is referred to as the *intrinsic rate of natural increase* and so we have a population growth function:

$$N_t = N_0\, e^{rt}, \tag{10}$$

which is known as the Malthusian growth model (Roberts, 2010, p 131) typical of populations growing with unlimited resources.

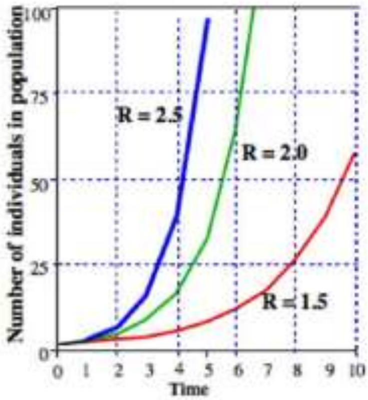

Figure 1. General form of exponential growth of a population in (8) (Vandemeer, 2010).

Consider starting from a single individual and so $N_0 = 1$. We have:

$$N_t = e^{rt},$$

and so

$$\ln N_t = rt. \tag{11}$$

The natural logarithm of the population number is equal to the intrinsic rate of increase, *r*, by time. Many micro-organisms closely follow this exponential pattern of growth which can also be written as:

$$\frac{d \ln N_t}{d t} = r , \tag{12}$$

showing that the growth rate of the log of the population number is the intrinsic rate of increase. This can then be rewritten (now omitting the subscript *t* for simplicity) more intuitively as:

$$\frac{d}{dt}(\ln N) = \frac{1}{N}\frac{dN}{dt} = r$$

$$\text{or } \frac{dN}{dt} = rN \tag{13}$$

$$\left(\text{since } \frac{d\ ln\ N}{d\ N} = \frac{1}{N} \quad \text{or} \quad \int \frac{1}{N} dN = ln\ N + C\right).$$

We can note also that *r* and *R* are related as:

$$R = e^r \text{ and so } r = ln\ (R).$$

.

We now proceed to show that the exponential equation, as a model of population dynamics, requires modification to account for the empirical fact that intrinsic rates of population increase, *r*, tend to decrease while (and even because) a population size is increasing, thus leading to the Logistic Equation.

Logistic Equation

Population growth rate

Empirically, the intrinsic growth rate, *r*, tends to decrease as *N* increases as a result of what is known as *density dependence* in the behavior of populations. There is found to be a general relation between intrinsic rate of increase and population density, which can be approximated by a straight line (Figure 2).

Thus, we can now express *r* in the form: *r* = *f(N)* and modify (10) as

$$\frac{dN}{dt} = f(N)N\ .$$

Given the straight line empirical result that *r* decreases as population density increases, we can represent *f(N)* as *a* – *bN* where *a* is the *r* axis intercept and *b* the rate of decrease of *r* giving:

$$\begin{aligned}\frac{dN}{dt} &= f(N)N \\ &= (\mathrm{a - bN})\mathrm{N} \\ &= \mathrm{aN - bN}^2 \qquad (14)\end{aligned}$$

which is an expression of the **logistic equation** (Roberts, 2010. P 133).

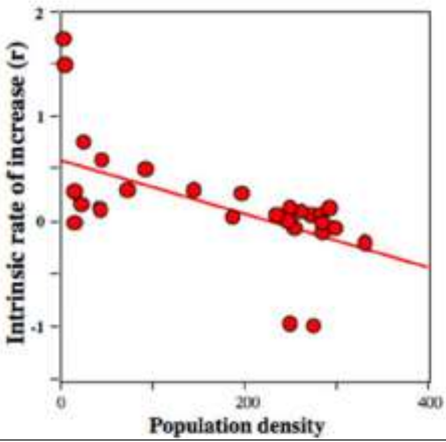

Figure 2. Empirical evidence, from a laboaratory population of paramecium, that intrinisic rate of population increase descreases as population density increases (Vandemeer, 2010).

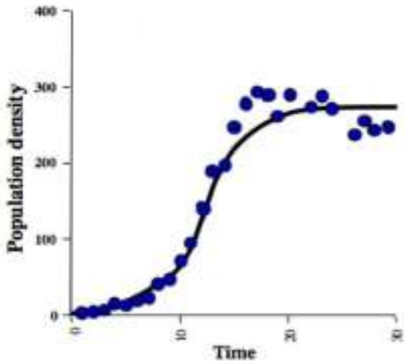

Figure 3. The logistic pattern showing an initial exponential growth pattern for the laboaratory population of paprmecium (Figure 1) followed by a decreasing growth rate caused by environmental limitations (Vandemeer, 2010).

We note that, when growth rate is zero, this becomes a quadratic equation when $\frac{dN}{dt} = 0$ giving:

$$aN - bN^2 = 0,$$

or

$$N(a - bN) = 0, \qquad (15)$$

and so when $N = 0$ or $N = a/b$. These results and empirical evidence (Figure 3) already suggest a sigmoid growth function with a minimum, maximum and point of inflection (Figures 4, 5, & 6).

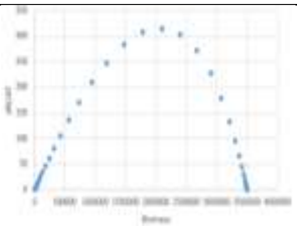	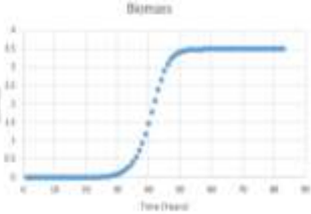	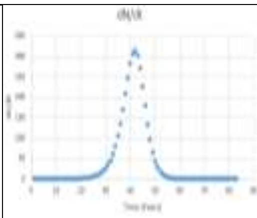
Figure 4. Quadratic growth rate function, *dN/dt*, as a function of total biomass of a population.	**Figure 5.** Sigmoid Growth function (c.f. Figure 3) as a function of time. The point of inflection is shown as the maximum in Figure 4.	**Figure 6.** Growth rate function, *dN/dt*, as a function of time again showing a maximum (c.f. the point of inflection in Figure 5).

An alternative form of the logistic equation for population growth can be obtained by assuming that the growth rate is proportional to the relative amount of living space available to the population and introduce the term **carrying capacity** with symbol *K*. Thus, intrinsic growth rate *r* can be modified as:

$$r\frac{(K-N)}{K} = rN - \frac{r}{K}N^2 = rN\left(1-\frac{N}{K}\right)$$

to account for the linear decrease in *r*, proportional to the increase in N. The result is a logistic equation for population growth:

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right) \qquad (16)$$

which also has the form $aN - bN^2$. Thus, we can now give *a* and *b* intuitive biological meaning with *a* = *r* and *b* = *r/K*, the latter known as the braking term.

Fish growth model

The von Bertalanffy fish growth model (1951) is also based on the logistic equation and is given by:

$$L_t = L_\infty\left(1-e^{-K(t-t_0)}\right) \qquad (17)$$

where L_t is fish length at time *t*, L_∞ is **asymptotic length** or the mean length that individuals in a given stock would reach if they were to grow indefinitely, k is the **growth rate** parameter, the rate at which L_∞ is approached, and t_0 is the **age** of the fish at zero length if it had always grown according to the equation.

The model assumes a length celling or theoretical maximum length similar to a population ceiling which is determined by density dependence. Instead of density dependence, here we have physiologic constraints on growth size determined by genetic structure. The model also assumes fish grow to a theoretical maximum length (or weight) and the closer the length gets to this maximum the slower will be the rate of change of length, an assumption which gives good fits to empirical data (Figure 7).

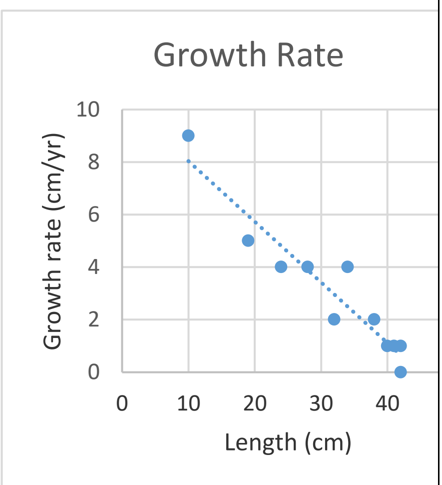

Figure 6. Straight line empirical growth rate data calculated from empirical data presented in Figure 7 and suggesting, that intrinisic rate of population increase, descreases as population density increases.

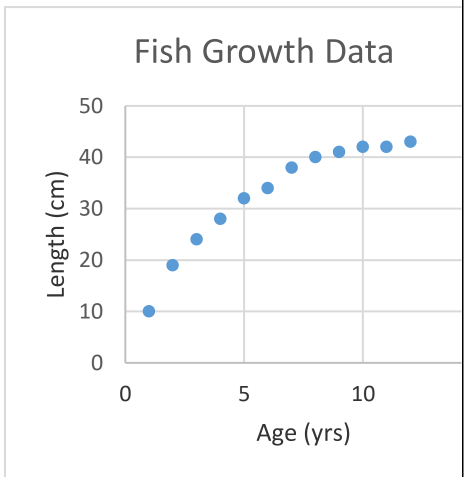

Figure 7. Evidence of the logistic pattern. Initial growth pattern for fish because data are available only for fish large enough to be caught. Shown is the decreasing growth rate caused by genetic constraints (Cubillos, 2017).

To make equation (17) more intuitively obvious we can relate it to equation (9) of the exponential model as follows:

From (17) $$L_t - L_\infty = -L_\infty e^{-K(t-t_0)}$$

and so $$\frac{L_\infty - L_t}{L_\infty} = e^{-K(t-t_0)} \text{ or } \frac{1}{e^{K(t-t_0)}}$$

which is the remaining fraction of total growth available as t increases.

$$\ln\left(\frac{L_\infty - L_t}{L_\infty}\right) = -K(t - t_o)$$

$$\frac{\mathrm{d}\,\dfrac{\ln\left(\mathrm{L}_\infty - L_t\right)}{\mathrm{L}_\infty}}{dt} = -K$$

where $\frac{L_\infty - L_t}{L_\infty}$, remaining fraction of growth, replaces population $N(t)$ and -K replaces r in (12) (c.f. $\frac{\mathrm{d}}{\mathrm{d\,t}}(\ln\ \mathrm{N}_t) = r$). Again, we can note from (12) that:

$$\frac{d\ \mathrm{L}_t}{\mathrm{dt}} = L_\infty K e^{-K(t-t_0)}$$
$$= \mathrm{K}(\mathrm{L}_\infty - L_t)$$
$$= \mathrm{KL}_\infty \text{ - } \mathrm{KL}_t$$
$$= \mathrm{a - bL}_t$$

where a and b are constants and the rate of increase of L_t with time is assumed to be a linear function of L_t, a relation which can be empirically verified (Figure 6). Again, we have the form of the logistic equation.

Having considered these examples (population and size growth rate functions) we now proceed to formalize the logistic equation.

Logistic Models of Population Growth

The logistic or Verhulst (Roberts, 2010, p133**)** equation has already been derived as (Equation (16)):

$$\frac{dN}{dt} = rN - r\frac{N^2}{K}$$

which can be interpreted as the change of rate of population N = birth rate – death rate, and where r is intrinsic rate of increase, K is carrying capacity, and N (or $N(t)$) is the number of individuals at time t. This is a differential equation of the form:

$$y' \text{ or } dy/dt = ay - by^2 \tag{18}$$

where b is the "braking" term r/K, and a is the growth term r.

We note that Equation (13) can also be expressed in terms of **biomass** instead of population size:

$$\begin{aligned}\frac{dB}{dt} &= rB(t) - rB(t)^2 / K \\ &= \mathrm{rB(t)}\left(1 - \mathrm{B(t)}\right) / K\end{aligned} \tag{19}$$

where $B(t)$ is population biomass and where maximum biomass $B\,\infty$ is constrained again by carrying capacity, K.

The logistic equation (16) can be shown (Kreyszig, 2011, p32) to have the solution:

$$y = \frac{1}{ce^{-at} + \frac{b}{a}} \tag{20}$$

which reduces to the exponential function $\frac{1}{c}e^{At}$ for $b=0$ (unlimited carrying capacity). Thus (16) will have the solution:

$$N_t = \frac{1}{ce^{-rt} + \frac{1}{K}}\;. \tag{21}$$

Here we have self-limiting population growth (Figure 8) determined by carrying capacity K of the supporting environment. The logistic growth function solution for various values of c as shown in the legend. Growth term (a or r) is set at 8, breaking term (b or r/K) at 2 and so equilibrium position at 4 (a/b or K). For $N_0 < K$, $c > 0$ and population grows initially exponentially before the braking term becomes dominant and equilibrium (carrying capacity) is reached. For $N_0 > K$, $c < 0$ and population is not sustainable, braking term is dominant and population is reduced to carrying capacity, K.

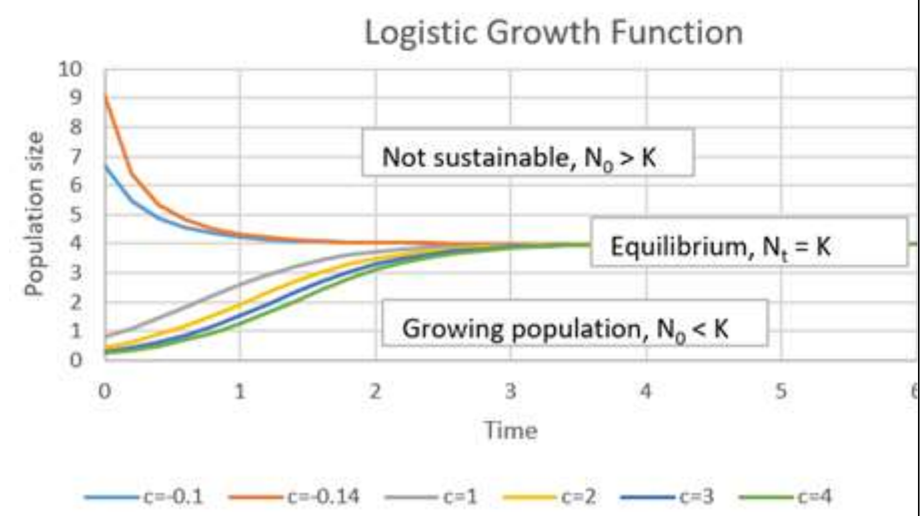

Figure 8. The logistic growth function solution for various values of *c* as shown in the legend. Growth term (*a* or *r*) is set at 8, breaking term (*b* or *r/K*) at 2 and so equilibrium position at 4 (*a/b* or *K*). For $N_0 < K$, $c > 0$ and population grows initially exponentially before the braking term becomes dominant and equilibrium (carrying capacity) is reached. For $N_0 > K$, $c < 0$ and population is not sustainable, braking term is dominant and population is reduced to carrying capacity, *K*.

Logistic Update Function

The logistic function can also be expressed as an update or difference function:

$$N_{t+1} = N_t + rN_t\left(1 - \frac{Nt}{K}\right) \qquad (22)$$

by approximation using $\frac{N_{t+1} - N_t}{N_t}$ to replace $\frac{dN}{dt}$ and where N_t represents population number at time *t*.

Logistic Function with harvesting

Here we modify equation (20) as:

$$y' = ay - by^2 - Hy$$

$$= (a - H)\,y - by^2 \qquad (23)$$

where *Hy* is an equilibrium or sustainable harvest and *H*, (where $H < a$ to avoid extinction and allow renewable harvesting), is harvesting rate (catch size over a given period of time) as it effectively reduces growth rate. The corresponding ODE solution, as a modification of (20), becomes:

$$y = \frac{1}{ce^{-(a-H)t} + \dfrac{b}{a-H}} \quad . \qquad (24)$$

The equilibrium position (figure 9) now changes from a/b to *(a – H)/b*

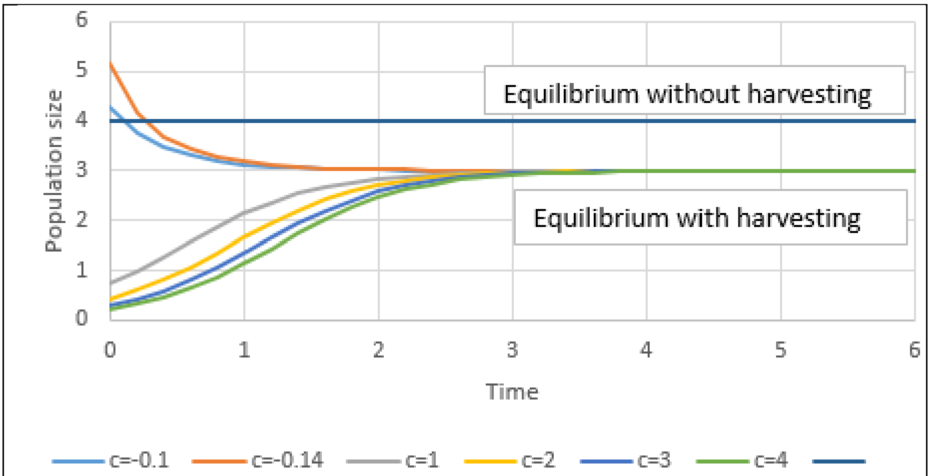

Figure 9. The logistic growth function solution with harvesting using the values of *a*, *b* and *c* in figure 8, a harvesting rate of H = 2 has been added. The equilibrium position drops from 4 without harvesting to 3 with harvesting. If harvesting were to cease for a sufficiently long period of time, the original equilibrium position would be restored.

Intermittent harvesting

Here we consider a simplified situation (Kreyszig, 2011, p 36, Qns. 37, 38 and 39) where $a = b = 1$ and $H = 0.2$ to develop a model to illustrate sustainable harvesting.

Equation (19) becomes:

$$y' = (1 - 0.2)y - y^2 , \qquad (25)$$

and equation (20) becomes:

$$y = 1/(1.25 - 0.75\, e^{-0.8t}). \qquad (26)$$

The equilibrium position without harvesting will be *a/b* or 1, and with harvesting will occur as $t \rightarrow \infty$, giving y = 1/1.25 or 0.8 (Figure 10).

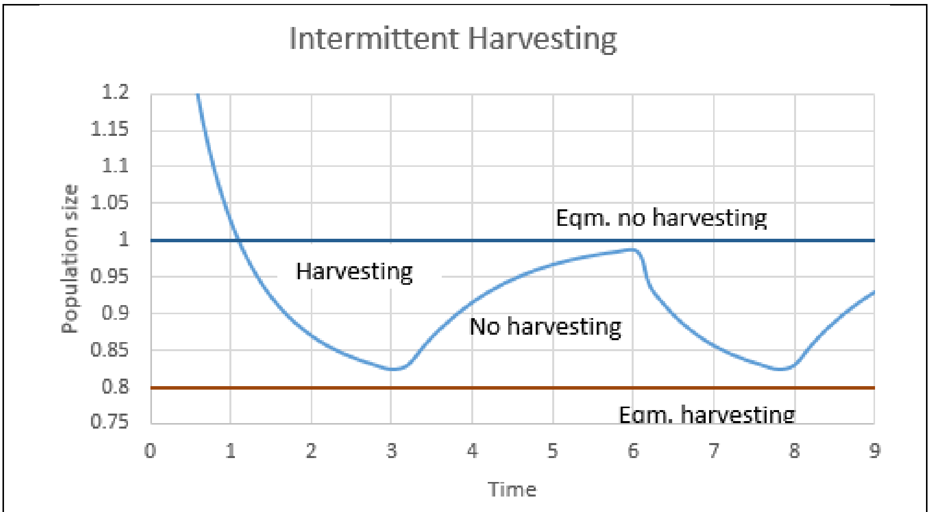

Figure 10. The logistic growth function solution with intermittent harvesting using the values a = b = 1 and H = 0.2. After an initial 3 unit time span when a harvesting equilibrium is reached, there follows an equal time span without harvesting when a higher equilibrium is reached. This process can be regarded as a predator-prey model and represents a system of sustainable harvesting.

Here we can illustrate a model for intermittent and sustainable harvesting (Figure 10). An initial period of harvesting when an equilibrium is reached, there follows an equal time span without harvesting when the fishery is rested and a higher equilibrium is reached. This process can be regarded as a predator-prey model and represents a system of sustainable harvesting as population size oscillates within two equilibrium boundaries.

Local species extinction

Population below critical mass

Here we consider Nurgaliev's Law (http://www.nature.com/scitable/knowledge/library) which relates the rate of change of the size of a population at a given time to population size:

$$\frac{dN}{dt} = BN^2 - AN \;\; or \;\; y' = By^2 - Ay, \qquad (27)$$

$$\text{(birth rate - death rate)}$$

where B is a birth rate proportionality constant, A is the corresponding death rate constant, and N or y is population size. Birth rate, B, is the probability of individuals of one gender (half the population) finding a mating contact with a member of the opposite gender.

By analogy with equation (20), we can form a solution to this ODE as:

$$y = \frac{A}{cAe^{At} + B}. \tag{28}$$

We can notice from equation (23) that $y' = 0$ (equilibrium) when $By(y-A/B) = 0$ or $y = 0$ or A/B as can be verified from Figures 11 and 12.

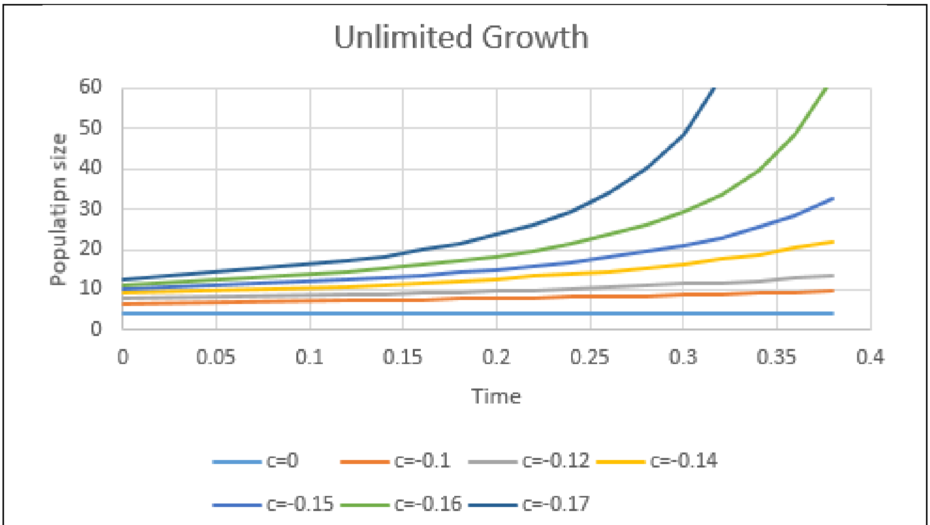

Figure 11. Using Equation (24) with $A = 4$, $B=1$ and values of c as shown in the legend, we find an initial period of unlimited growth of the population when $y > A/B$ or 4. This initial period, of course, must eventually be followed by a period when the population density braking term takes effect.

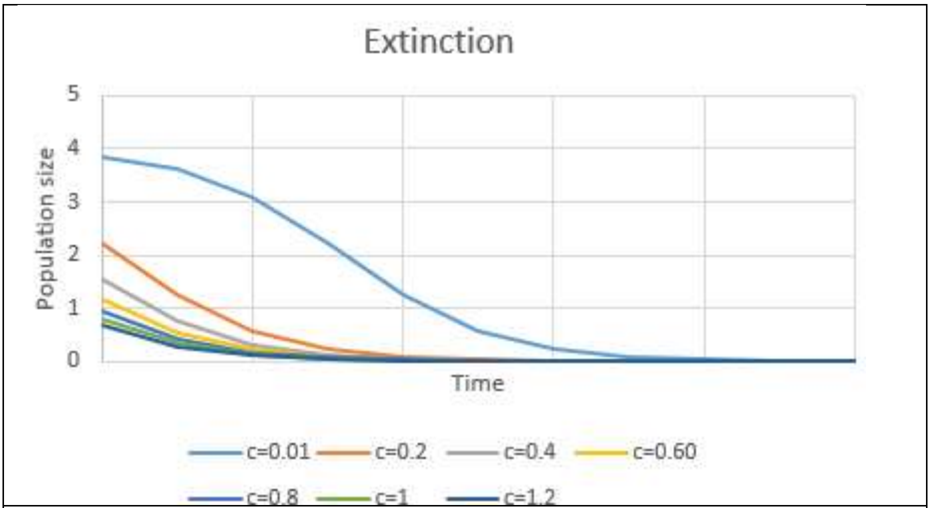

Figure 12. Using Equation (24) with $A = 4$, $B = 1$ and values of c as shown in the legend, we find a decrease in population when $y < A/B$ or 4 leading to extinction.

We can also notice three different cases arising from Equation (23):

(i) if $y' > 0$, $By^2 > Ay$ and so $y > A/B$ (Figure 11);
(ii) if $y' < 0$, $Ay > By^2$ and so $y < A/B$ (Figure 12);
(iii) if $y' = 0$, $By^2 = Ay$ and so $y = A/B$ (blue line in Figure 11).

For case (i) we have unlimited growth, at least initially and before density dependence takes effect, and for case (ii) we have progression to zero population and so local species extinction. A physical interpretation of (ii) is that the initial population is so low that individuals of the species are so sparsely distributed that they have difficulty finding mating partners. Thus we also have the concept of a critical population mass required for species survival.

Overharvesting

Local species extinction can also result from a level of harvesting leading to population dropping below a certain critical level. Here we consider equation (16) with a harvesting term added:

$$\frac{dN}{dt} = rN - r\frac{N^2}{K} - H \qquad (29)$$

where $N = N_t$, the population at time t, and H is now the harvesting rate expressed as catch size per unit of time. At equilibrium, $dN/dt = 0$ which gives rise to the quadratic equation:

$$0 = -rN^2/K + rN - H, \quad (30)$$

which will have real solutions when (using the well–known quadratic formula result $b^2\text{-}4ac \geq 0$):

$$r^2 - 4(-r/K)(-H) \geq 0,$$

whence

$$r^2 \geq 4(rH/K),$$

or

$$H \leq r^2 K/4r.$$

At a harvest rate greater than this, there will be no (real number) solutions to the quadratic, so no equilibrium population reached (dN/dt will never $= 0$), and this level of harvesting will again lead to local extinction of the species.

We can note that for a single real solution to equation (30), ($b^2 - 4ac = 0$), the population size will be a minimum value ($-b/2a$ from the quadratic equation solution):

$$N = -r/(-2r/K) = K/2.$$

Thus, the smallest population remaining after harvesting which will avoid the population going to extinction is half the carrying capacity, K. Again, this can be interpreted as the population density falling below a critical mass such that individuals of the species cannot find a sufficient number of mating partners to sustain a viable population.

Summary and Conclusion

This paper was developed in the context of the need for growth models for sustainable fisheries. It has initially noted certain invariant properties of the exponential function which make it suitable for modelling initial growth of populations, at least until the constraints of population density and harvesting take effect and the logistic equation will be required. The logistic equation, a first order linear ODE based on empirical data, was shown to model both fish size growth and population growth. The solution to the ODE has shown that, in a given fishery, for example, there can exist an equilibrium population towards which both larger (non-sustainable) and smaller (growing) populations will tend (Figure 8). The logistic equation modified to account for harvesting produces a reduction in the equilibrium population (Figure 9). Intermittent harvesting (Figure 10) shows sustainable harvesting with population oscillating between two equilibrium positions when periods of harvesting are separated by periods of resting. Finally, local extinction of species was shown to occur when a population falls below certain critical values such as when only birth and death rates are considered (Figures 11 and 12) for initial growth and secondly when the level of harvesting is such that population falls below half the carrying capacity of the fishery. In both cases the interpretation can be made that population density is so low that individuals cannot find sufficient number of mating partners to maintain a positive growth rate.

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Authors' Details

Professor Peter K. Anderson, Ph.D.,
Head, Department of Information Systems, and
Head, Department of Mathematics & Computing Science,
Divine Word University, Madang (PNG),
Email: panderson@dwu.ac.pg