MATH3070
Natural Resource Mathematics
Week 1 Lecture Notes

These notes are M.H. Holden's and J. A. Filar's summary of selected sections from C.W. Clark., *"Mathematical Bioeconomics: The Mathematics of Conservation"*, 3rd ed., Wiley, 2010, along with additional supplementary material we developed from our own expertise in natural resource mathematics.

Before we begin, I would like to introduce two scientific folklore concepts that are central to this course:

"Occam's Razor" sometimes called the "law of parsimony"

Quoting from Wikipedia: This is a problem-solving principle attributed to William of Ockham (c. 1287-1347), who was an English Franciscan friar, scholastic philosopher, and theologian. His principle can be interpreted as stating: Among competing hypotheses, the one with the fewest assumptions should be selected. Arguably, this concept was only slightly qualified some 700 years later in a quote often attributed to Einstein: "Everything should be made as simple as possible, but not simpler".

"Tragedy of the commons"

Again, quoting from Wikipedia: This is a theory attributed to an 1833 essay by a Victorian economist William Forster Lloyd: It addresses an economic theory of a situation within a shared-resource system where individual users acting independently according to their own self-interest behave contrary to the common good of all users by depleting or spoiling that resource through their collective action.

1 Natural Resource Mathematics

In these notes I shall follow the basic structure of C.W. Clark's *"Mathematical Bioeconomics: The Mathematics of Conservation"*, Wiley, 2010, third edition. I shall use similar notation to that used by Clark but shall supply more detailed derivations plus supplementary material in various sections.

Since this course focuses on mathematical models of natural resources, it is useful to reflect on the fundamental question of what can or cannot be captured with a mathematical model. Section 1.2 of Clark's book touches on this. However, I would also refer you to:

- Otto and Day (2007) A Biologist's Guide to Mathematical Modeling in Ecology and Evolution. Princeton Univ. Press to 3.2,

which will be a good supplement for those who want more biological motivation. It will also be used in the some of the later parts of this course.

Some of the key points to remember when working with mathematical models of natural phenomena are:

- Most models constitute a greatly simplified description of the studied phenomenon.

- Models' variables and parameters do not know what they're supposed to represent. Their "allegiance" is only to logical consistency of mathematical expressions rather than the modellers' notions of what these expressions are intended to capture.

- A model requires a domain in which it can be applied with reasonable confidence that its outputs will be interpretable in the intended manner.

- A model must be accompanied by a complete list of assumptions used in its design.

Note: there are also instances where nature imitates a mathematical model. For instance, the equation $x^2 + y^2 = r^2$ is an abstract description of a "perfect circle" and all circles we can draw or observe in nature are merely approximations to that abstract description.

Depending on your religious beliefs you may, or may not, subscribe to Galileo's famous quotation:

"Mathematics is the language in which God has written the universe." (1564-1642)

However, irrespective of your religious beliefs, you must agree that much of our scientific knowledge and understanding has been written down in the language of mathematical models. Just look at engineering, economics, biology, physics or chemistry journals.

Of course, in this course, we shall focus on mathematical models as they pertain to human interactions with natural resources. In particular, models of fisheries will play a central role

but it must be stressed that similar models also apply to other biological population models impacted by external inputs.

One of the simplest **exponential growth** (or **density-independent**) population growth models is captured by the equation

$$\frac{dx}{dt} = \dot{x}(t) = rx(t); \qquad x_0 = x(0). \tag{1}$$

Note: sometimes the argument t is suppressed and the model is written simply as $\dot{x} = rx$; x_0.

Of course, t, x and r "don't know what they are", but, in our context, t is a nonnegative variable denoting time; $x(t)$ denotes the size of some population at time t; x_0 is the inital size of the population and r is a parameter denoting the **intrinsic growth rate** of the population.

You probably already know how to solve (1), but, for the record, as long as $x(t) \neq 0$ we can set

$$\frac{\dot{x}(t)}{x(t)} = r,$$

and integrate both sides w.r.t. t recalling that only $x(t) > 0$ is of interest, namely

$$\int \frac{\dot{x}(t)}{x(t)} \, dt = \int r \, dt$$
$$\Rightarrow \ln[x(t)] = rt + c \qquad \text{(where c is a constant)}$$
$$\therefore \ x(t) = e^{rt}e^{c}.$$

Substituting the boundary condition $x_0 = x(0)$ yields $x_0 = x(0) = e^0 e^c \Rightarrow e^c = x_0$. That is,

$$x(t) = x_0 e^{rt}; \qquad t \geqslant 0. \tag{2}$$

Now, assuming that $x_0 > 0$, the solution function takes three alternative shapes, depending on whether $r > 0$, $r = 0$ or $r < 0$.

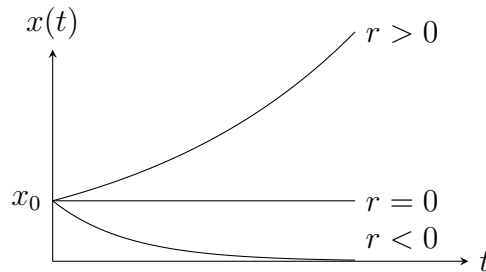Figure 1

This is because:

$$r = 0 \overset{(1)}{\Rightarrow} x(t) = x_0 \qquad\qquad\qquad \text{(alternatively, } \dot{x}(t) = 0)$$

$$r > 0 \Rightarrow e^r > 1 \overset{(2)}{\Rightarrow} x(t) = x_0 e^{rt} = x_0 (e^r)^t \to \infty \qquad \text{(alternatively, } \dot{x}(t) = rx(t), r > 0)$$

$$r < 0 \Rightarrow e^r < 1 \overset{(2)}{\Rightarrow} x(t) = x_0 e^{rt} = x_0 (e^r)^t \to 0 \qquad \text{(alternatively, } \dot{x}(t) = rx(t), r < 0)$$

Obvious question: Does (1) make sense as a biological population model? We **cannot change** the fact that $x(t) = x_0 e^{rt}$, $t \geqslant 0$, is **the correct solution** of (1).

The **obvious answer** that (1) is clearly a bad model of a biological population of a species (because populations don't grow to infinity and, generally, don't become extinct) is too simplistic. But this view is also too simplistic, there can be periods of time when some populations fit each of the three modes of $x(t) = x_0 e^{rt}$ rather well. For instance, the population of

(a) Rabbits in Australia may well have followed the shape of $x_0 e^{rt}$ with $r > 0$ for a long stretch of time after Europeans brought them here.

(b) Population of northern quoll in Queensland may have exhibited characteristics of $x_0 e^{rt}$ with $r < 0$ for a period after cane toads were introduced around 1940.

(c) Some populations may be remarkably stable. For instance, Iceland, Portugal and Poland have close to zero population growth ($r = 0$).

We must remind ourselves of Einstein's quote "Everything should be made as simple as possible, but not simpler." Indeed, exponential growth is a simple model, with an elegant mathematical solution that is easy to understand. There will be applications where using exponential growth is appropriate, even highly desirable. For example, we will talk about invasive species, pest organisms that invade, establish and spread within a location where they were previously absent. The rabbits above are a good example of an invasive species, so are cane toads. Later in this course we will discuss how exponential growth models can be useful for deriving management strategies for invasive species, given a set of specific assumptions.

2 Discrete Time Models

Semelparous fish species (possessing only a single reproductive episode before death) tend to have a life cycle consisting of migration:

spawning in lakes/streams $\rightarrow$ ocean (where they mature) $\rightarrow$ original fresh waters to spawn and die.

Pacific salmon is a prime example of such a species.

However, if they are commercially harvested in the ocean phase it is clear that discrete time step from cycle to cycle is a natural time domain. In this section, time stages/cycles will be denoted by $t \in \{0, 1, 2, \dots\}$.

Remarks: Let us define the following, new, notation:

R_t = recruitment of adult fish to the fishery in cycle t

H_t = catch taken from R_t in cycle t

$S_t := R_t - H_t$ = escapement from the fishery in cycle t (survivors of fishing).

Importantly, we define the function, $F(\cdot)$, called the **spawner-recruit relationship**, such that
$$R_{t+1} = F(S_t) = F(R_t - H_t); \ t = 0, 1, \dots \tag{SR}$$
where S_0 = initial escapement population (must be given). Note that any natural mortality (due to birds, bears, disease, other predators) is incorporated in the function F. Note that:

(i) If the fishery has converged to an equilibrium, then $S = S_t = S_{t+1} = S_{t+2} \dots$ and it is possible to study equilibrium properties from the properties of $F(S)$.

(ii) At equilibrium $R = R_t = R_{t+1} = R_{t+2} \dots$ and $H = H_t = R_t - S_t = H_{t+1} = R_{t+1} - S_{t+1} \dots$, namely

$$R = R(S) = F(S) \qquad \text{and} \qquad H = H(S) = R - S = F(S) - S. \tag{SS}$$

(iii) For discrete models it is customary to define the carrying capacity $K > 0$ for spawners as the solution of the equilibrium equation $S = F(S)$, assuming that a non-trivial asymptotically stable equilibrium exists.

Two famous discrete-time models are characterized by the form of $F(S)$.

Ricker Model uses
$$F(S) = aSe^{-bS}, \tag{RM}$$
where parameters $a, b > 0$ can be chosen to best fit the data. See Figure (8).

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Beverton-Holt Model uses
$$F(S) = \frac{aS}{b+S},\tag{BHM}$$
where, once more, parameters $a, b > 0$ can be chosen to best fit the data. See Figure (9).
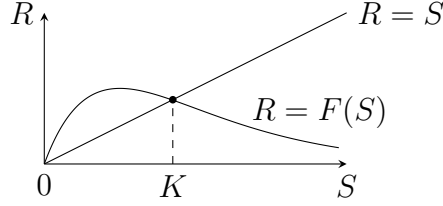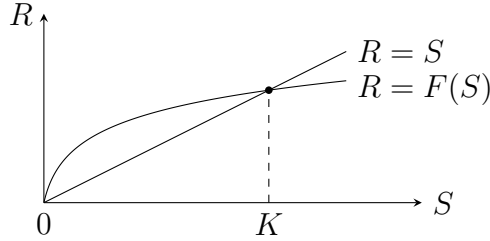

Figure 2: Ricker Recruitment Relationship

Figure 3: Beverton-Holt Recruitment Relationship

Figures (2) and (3) exhibit typical shapes of the spawner-recruit functions in the Ricker and Beverton-Holt models respectively.

The feature that, in the Ricker model $F(S)$, begins to decay for S large enough is called the property of **overcompensation**. It implies that large escapement leads to lower recruitment (perhaps, because of biological overcrowding). This may, or may not, occurr for the species of interest.

Beverton-Holt model with zero harvest $(H_t = 0)$

Equation (SR) reduces to $R_{t+1} = F(R_t) = \dfrac{aR_t}{b+R_t}$, $t = 0, 1, \ldots$, or equivalently

$$R_t = \frac{aR_{t-1}}{b+R_{t-1}}, \quad t = 1, 2, \ldots \tag{BH$_0$}$$

Interestingly, with inital cohort R_0 given, the above difference equation has a closed form solution which can be derived as follows:

$$\frac{1}{R_t} = \frac{b+R_{t-1}}{aR_{t-1}} = \left(\frac{b}{a}\right)\frac{1}{R_{t-1}} + \frac{1}{a}, \quad t = 1, 2, \ldots$$

Setting, $y_t = \dfrac{1}{R_t}, y_0 = \dfrac{1}{R_0}, \gamma = \dfrac{b}{a}, \alpha = \dfrac{1}{a}$ the above reduces to

$$y_t = \gamma y_{t-1} + \alpha; \quad y_0; \quad t = 1, 2, \ldots \tag{58}$$

But (58) is a linear difference equation which can be iterated as follows

$$
\begin{aligned}
y_t &= \gamma y_{t-1} + \alpha = \gamma(\gamma y_{t-2} + \alpha) + \alpha = \gamma^2 y_{t-2} + \gamma\alpha + \alpha \\
&= \gamma^2(\gamma y_{t-3} + \alpha) + \gamma\alpha + \alpha = \gamma^3 y_{t-2} + \gamma^2\alpha + \gamma\alpha + \alpha \\
&= \cdots = \gamma^t y_0 + \alpha(\gamma^{t-1} + \gamma^{t-2} \cdots + 1) \\
&= \gamma^t y_0 + \frac{\alpha(\gamma^t - 1)}{\gamma - 1},
\end{aligned}
\tag{59}
$$

provided that $\gamma \neq 1$ (a very mild assumption). That is

$$y_t = \frac{y_0 \gamma^t (\gamma - 1) + \alpha(\gamma^t - 1)}{\gamma - 1},$$

which on reverting back to R_t becomes

$$R_t = \frac{R_0(1 - \gamma)}{\gamma^t(1 - \gamma) + \alpha R_0(1 - \gamma^t)}, \quad t = 1, 2, \ldots \tag{60}$$

It is left as an exercise to show that under a standard assumption of $a > b$, the intrinsic growth rate is $r = \dfrac{a}{b} - 1$ and the carrying capacity is $K = a - b$. Exercise; show that (60) can be transformed

$$R_t = \frac{K R_0}{R_0 + (K - R_0)\gamma^t}, \quad t = 1, 2, \ldots \tag{61}$$

Note that with $a > b, \gamma = \dfrac{b}{a} < 1$ and so $R_t \to K$ as $t \to \infty$, as expected, with zero harvest.

Stability of Equilibria

Definition: *An equilibrium R^* of the map F is stable if, given $\epsilon > 0$, there exists a $\delta > 0$, such that $|R_0 - R^*| < \delta$ implies $|F^n(R_0) - R^*| < \epsilon$, for all $n > 0$*

Theorem 1 *Let R^* be an equilibrium of the map defined by the continuously differentiable function F. Then R^* is stable if $|F'(R^*)| < 1$, and unstable if $|F'(R^*)| > 1$.*

3   General Production Model

Since populations of species do not grow to infinity in the wild (as would be the case in (2) if $r > 0$), the obvious temptation is to replace (1) by something more realistic which carries with it the notion of a **carrying capacity** of the environment.

Carrying capacity is an essential concept in ecology. Essentially it postulates the presence of a finite upper bound, K, on the size of the population that an ecosystem can support. Note that this too can be a controversial issue, but we shall accept it as a working assumption for most of this course.

A group of models that we shall consider in lieu of (1) have the generic form:

$$\dot{x}(t) = G(x) - h(t), \quad t \geqslant 0, \quad x(0) = x_0, \tag{GP}$$

where $G(x)$ can be thought of as the "natural" growth function and $h(t)$ is the **rate of removal (harvest)** function. GP stands for the **general production model**. Sometimes we shall write $h(x, t)$ instead of $h(t)$, when the harvest depends on x as well as t. Can you think why it should?

We shall impose the following conditions:

A. $x(t) \geqslant 0, \; h(t) \geqslant 0 \; \forall \, t \geqslant 0$

B. $K > 0$

C. $G(x) > 0 \;$ if $\; x \in (0, K)$ \hfill (G1)

$\quad G(0) = G(K) = 0$ \hfill (G2)

$\quad G''(x) < 0 \;$ if $\; x \in (0, K).$ \hfill (G3)

Note: (G3) assumes that $G(x)$ is at least twice differentiable, and strictly concave on $(0, K)$.

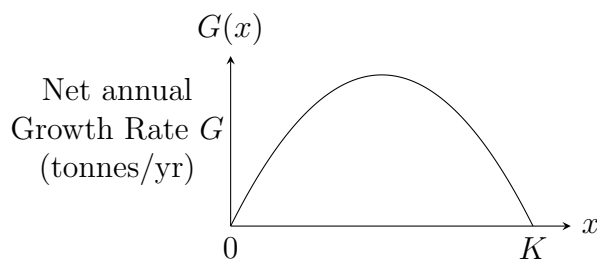Discussion: Under (G1) - (G3) the generic shape of $G(x)$ is displayed in Figure 2.

Figure 4

We assume that the model (GP) loses ecological relevance if $x \notin [0, K]$ because: (a) $x < 0$, negative population is meaningless and (b) $x > K$ population exceeding carrying capacity is "impossible". Why is (b) potentially controversial? Read about the "Malthusian trap".

Frequently, we shall consider the zero harvest case where $h(t) \equiv 0 \ \forall \ t \geqslant 0$, that is

$$\dot{x}(t) = G(x), \qquad x(0) = x_0 \tag{GP0}$$

that is intended to illustrate the populations behaviour without human interference (discussion?).

It can be shown formally that, in (GP0), if $x_0 \in (0, K)$, then

$$\lim_{t \to \infty} x(t) = K. \tag{3}$$

More generally, we shall say that the **equilibrium point** x^* such that $G(x^*) = 0$ is:

(i) **stable** if all solutions $x(t)$ of (GP0) with x_0 sufficiently near x^* satisfy $\lim_{t \to \infty}[x(t)] = x^*$.

(ii) **unstable** if all solutions $x(t)$ of (GP0) with x_0 near x^* do not approach x^*.

(iii) **semistable** if initial conditions x_0 on one side of x^* lead to solutions $x(t)$ that approach x^* as $t \to \infty$, while initial conditions x_0 on the other side of x^* lead to solutions $x(t)$ that do not approach x^* as $t \to \infty$.

Note that in view of (3), $x^* = K$ is a **stable equilibrium point** of (GP0) and that it can be easily shown that $x^* = 0$ is an **unstable equilibrium point** of (GP0).

Recall that by Taylor's theorem, for ε sufficiently small

$$G(x^* + \varepsilon) \approx G(x^*) + G'(x^*)\varepsilon + \frac{1}{2}G''(x^*)\varepsilon^2. \tag{4}$$

We can exploit (4) to demonstate that in (GP0) $x^* = K$ is a stable equilibrium and $x^* = 0$ is an unstable equilibrium (see Assignment 1).

4 The Logistic Model

This is a very famous special case of (GP0) where

$$G(x) = rx\left(1 - \frac{x}{K}\right),$$

which leads to

$$\dot{x}(t) = \frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right), \quad x_0 = x(0) \in (0, K). \tag{LM}$$

It is sometimes called the **Verhulst model** recognizing the Belgian mathematician who studied it in the 1830's and used it to estimate the (human) US population in 1840 to within 1%.

Note:

(i) It is less clear where the name "logistic" originated. However, as will be seen below, the properties of the logarithmic function are used to derive a closed form solution of (LM).

(ii) Note that if $x \ll K$ then $G(x) \approx rx$ as in the exponential growth model. However, as $x \to K^-$, $G(x) \to 0$, thereby dramatically slowing the population growth as it approaches the maximal (carrying capacity) level.

(iii) Obviously $G(0) = G(K) = 0$ and $G''(x) < 0$ are satisfied.

Outline of solution of (LM)

First rewrite (LM) as

$$\frac{dx}{x\left(1 - \dfrac{x}{K}\right)} = r\ dt \iff \frac{dx}{x(K - x)} = \frac{r}{K}\ dt$$

and integrate the two sides of the above equation w.r.t. x and t, respectively, to obtain

$$\int \frac{dx}{x(K - x)} = \int \frac{r}{K}\ dt = \frac{r}{K}\ t + c_2, \tag{*}$$

where c_2 is a constant of integration.

Use partial fractions (or inspection) to verify that

$$\frac{1}{x(K - x)} = \frac{1}{Kx} + \frac{1}{K(K - x)} = \frac{1}{K}\left[\frac{1}{x} + \frac{1}{K - x}\right].$$

Hence LHS of (*) becomes (after lumping constants)

$$\int \frac{dx}{x(K-x)} = \int \frac{dx}{Kx} + \int \frac{dx}{K(K-x)} = \frac{1}{K}\left[\ln x - \ln(K-x) + c_1\right]$$
$$= \frac{1}{K}\ln\left(\frac{x}{K-x}\right) + \frac{c_1}{K}. \tag{**}$$

Combine (*) and (**) to obtain

$$\frac{1}{K}\ln\left(\frac{x}{K-x}\right) + \frac{c_1}{K} = \frac{r}{K}t + c_2,$$

$$\ln\left(\frac{x}{K-x}\right) = rt + (Kc_2 - c_1) = rt + \tilde{c}.$$

Next, eliminate logarithms by applying the exponential function (the inverse function of logarithm)

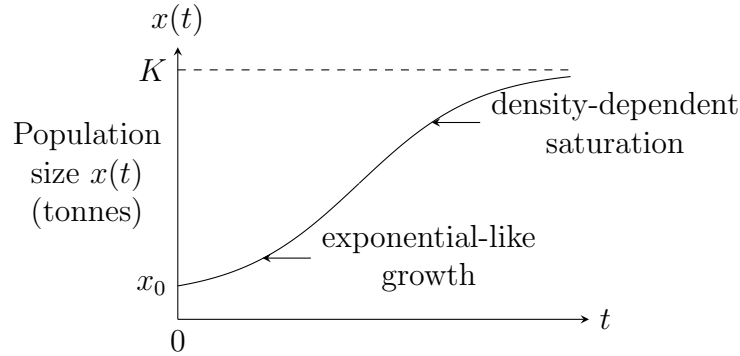$$\frac{x}{K-x} = \gamma e^{rt}, \qquad \gamma = e^{\tilde{c}}.$$

Figure 5

Solve the above for x

$$x = \gamma K e^{rt} - \gamma x e^{rt},$$

$$(1 + \gamma e^{rt})x = \gamma K e^{rt} \Rightarrow x = \frac{\gamma K e^{rt}}{1 + \gamma e^{rt}},$$

$$\Rightarrow x = x(t) = \frac{K}{\left(\dfrac{1}{\gamma e^{rt}} + 1\right)} = \frac{K}{1 + \dfrac{e^{-rt}}{\gamma}} = \frac{K}{1 + ce^{-rt}}, \tag{5}$$

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where $c = \dfrac{1}{\gamma}$ is a constant. Applying the boundary condition $x_0 = x(0)$

$$x_0 = \frac{K}{1 + ce^{-r0}} \overset{(exercise)}{\Longrightarrow} c = \frac{K - x_0}{x_0}.$$

Note: solution (5) is an "S-function" or a sigmoid curve (see Figure 3).

5   Maximum sustained (sustainable) yield

Let us return to the general production model

$$\dot{x}(t) = G(x) - h(t), \quad t \geqslant 0, \quad x_0 = x(0) \tag{GP}$$

where $h(t) \equiv h$, a constant harvest level at all times.

$$\dot{x}(t) = G(x) - h, \qquad t \geqslant 0, \quad x_0 = x(0) \tag{GPh}$$

Clearly, if $G(x) = h$ then $\dot{x}(t) = 0$ and the population is constant and hence such a harvest level could be called "sustainable", right? Well, it's a little more subtle than that, keep on reading!

With our generic, concave, production function $G(x)$, $G''(x) < 0$, we are going to have a unique maximum occurring at some x_M in $(0, K)$.

$$h_M : \ = \max_{0 \leqslant x \leqslant K} \big[G(x)\big] = G(x_M)$$
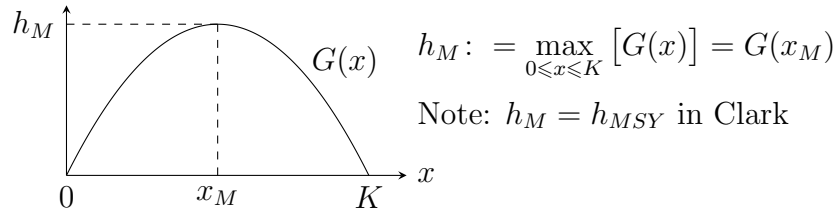
Note: $h_M = h_{MSY}$ in Clark

Figure 6

Note that h_M is usually called the *maximum sustained yield (MSY)* and $x_M = \arg\max_{x \in [0,K]}[G(x)]$ is the stock level corresponding to maximum sustained yield.

Clearly, if the constant harvest level is $h > h_M$, then $\dot{x}(t) = G(x) - h < 0 \ \forall \ t$ and the population will decrease to 0 (with increasing rapidity as it approaches extinction; why?)

The most naively tempting constant harvest level is

$$h_M = \max_{0 \leqslant x \leqslant K} G(x) \quad \because \quad \dot{x}(t) = G(x_M) - h_M = 0$$

and h_M maximizes the yield among all $h : G(x) = h$.

However, x_M is only a semi-stable equilibrium because if actual stock level is even slightly less than x_M the use of h_M will ensure that $\dot{x}(t) < 0$ and $x(t)$ will drift away from x_M ultimately towards 0 if h_M continues to be used. See also Assignment 1.
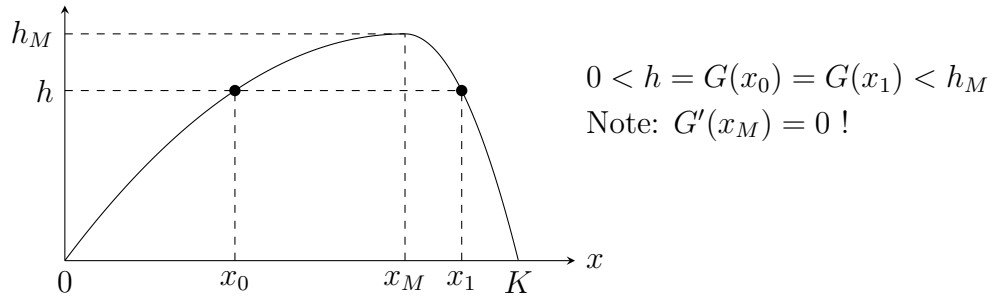
$$0 < h = G(x_0) = G(x_1) < h_M$$
Note: $G'(x_M) = 0$!

Figure 7

The third important case is when the constant harvest level satisfies $0 < h < h_M$, which corresponds to the situation portrayed in Figure 5, where there are two equilibria $x_0, x_1 \in [0, K]$ satisfying

$$0 < x_0 < x_M < x_1 < K.$$

Importantly, you will see from Assignment 1 problems that

(a) x_0 is an unstable equilibrium

   BUT

(b) x_1 is a stable equilibrium because if for small $\delta > 0$, $x = x_1 + \delta$, then $G(x_1 + \delta) - h < 0$ and the system tries to return to x_1 $\left(\dfrac{dx}{dt} < 0 \right)$. Similarly, if $x = x_1 - \delta$, then $G(x_1 - \delta) - h > 0$ and the system still tries to return to x_1 $\left(\dfrac{dx}{dt} > 0 \right)$.

Conclusion? If you're going to harvest at constant rate h, then according to (GPh), wait until you're pretty sure the stock x_1 is higher than x_M and harvest at the rate $h_1 = G(x_1)$.

Of course, that is easier said than done since we never know the stock precisely! Perhaps "higher" should be "sufficiently higher", but then what precisely should "sufficiently" mean? We will revisit this question when we get to the topics of statistics and stock assessments.

6 MSY in Discrete Time Models

Reminder from section 2, we have the following notation:

R_t = recruitment of adult fish to the fishery in cycle t

H_t = catch taken from R_t in cycle t

$S_t := R_t - H_t$ = escapement from the fishery in cycle t (survivors of fishing),

$R_{t+1} = F(S_t) = F(R_t - H_t),$

where F is the spawner-recruitment relationship. We define S_M = maximum sustainable escapement - corresponding to the maximum sustainable yield - and same as (Clark's S_{MSY}) by

$$S_M = \operatorname*{argmax}_{0 \leqslant S \leqslant K} \Big[H(S) \Big].$$

But differentiating constant H in (SS) means that

$$H'(S_M) = 0 \iff F'(S_M) - 1 = 0 \iff F'(S_M) = 1. \tag{57}$$

Namely, S_M is the point where the tangent of the spawner-recruit function is parallel to the straight line $R = S$.

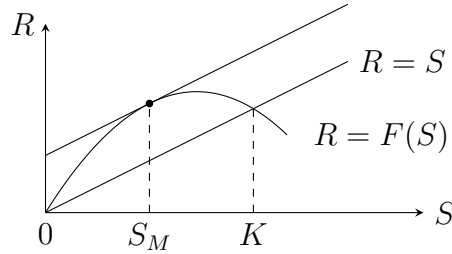Figure 8

Two famous discrete-time models are characterized by the form of $F(S)$.

Ricker Model uses

$$F(S) = aSe^{-bS}, \tag{RM}$$

where parameters $a, b > 0$ can be chosen to best fit the data. See Figure (8).

Beverton-Holt Model uses

$$F(S) = \frac{aS}{b + S}, \tag{BHM}$$

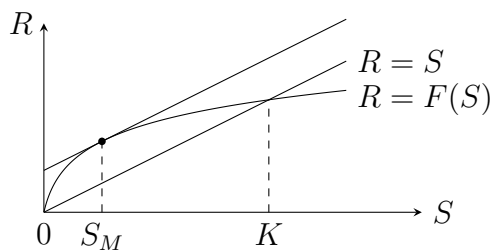where, once more, parameters $a, b > 0$ can be chosen to best fit the data. See Figure (9).

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Figure 9

Figures (8) and (9) exhibit typical shapes of the spawner-recruit functions in the Ricker and Beverton-Holt models respectively.

The feature that, in the Ricker model $F(S)$, begins to decay for S large enough is called the property of **overcompensation**. It implies that large escapement leads to lower recruitment (perhaps, because of biological overcrowding). This may, or may not, occurr for the species of interest.