3

The Dynamics of a Fishery

A fishery is an area with an associated fish or aquatic population which is harvested for its commercial or recreational value. Fishery can be wild or farmed. Fish are renewable resources because they reproduce, grow and die. In general, their stock level changes over an interval of time according to births, deaths and harvesting.

The FAO 2008 report on fisheries states that fish consumption has undergone major changes in the past four decades. Overall, consumption per person per year has been increasing steadily, from an average 9.9 kg in the 1960s to 16.4 kg in 2005. Despite the social and economic importance of fisheries, attempts at sustainable management have been unsuccessful in many parts of the world and a global response is urgently needed. An ecosystem approach to fisheries is called for, protecting and conserving ecosystems while providing food, income, and livelihoods from fisheries in a sustainable manner.

Many mathematical models have been developed to describe the dynamics of fisheries. Some of these are; the single-species models developed by Beverton and Holt, which are age- and size- structured, the van- Bertalanffy curve which considers growth in length of the fish, Beddington and May (1977), who considered the age structure and the growth of the fish populations and effects of fluctuations (Quinn and Deriso, 1999; Haddon, 2001). The simplest models assume a logistic equation for the fish population (R. Mchich, 2002). The fish depend on the natural food supply, so individuals compete for a limited food resource, and consequently their growth is dependent on population density.

3.1

Growth Model of a Fishery

We consider a fish population whose biomass is *n*. The natural growth process of the fish population can be given by

$$\frac{dn}{dt} = f(n) \qquad 3.1$$

Here *f (n)* is a representation of the births and deaths of the species in absence of harvesting. We assume that the fishery is a closed system. So there is no migration to and from the fishery. We assume a logistic growth for the natural growth of the fish population. Therefore, the natural growth of the population is given by

$$\frac{dn}{dt} = f(n) = rn(1-\frac{n}{K}) \qquad 3.2$$

Here *r* is the intrinsic growth rate of the biomass. It is the rate at which the population grows when *n* is close to zero. K is the carrying capacity (or saturation level) of the population. It represents the maximum population that the fishery can support.

Given an initial biomass $n(0)=n_0$, the fish population size at any time *t* is given by

$$n(t) = \frac{K}{1+(\frac{K}{n_0}-1)e^{-rt}} \qquad 3.3$$

The Growth Curve for the Fish Population

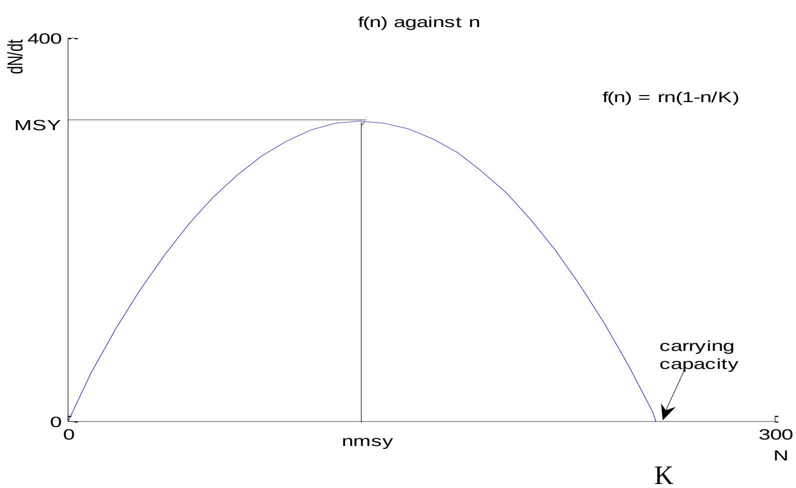

Figure 3.1. Plot of *dn/dt* against *n* to show the MSY.

From the diagram, it is clear that the growth function has a maximum point. We call this point MSY. When the stock size is at n_{msy}, the growth rate of the fish stock is at a maximum, and this maximum is referred to as the **maximum sustainable yield** – MSY (Figure 3.1).

We compute the maximum point (n_{msy}, MSY) of the curve. This is done by differentiating *f (n)* and equating it to zero.

$$f^{'}(n) = rn(\frac{-1}{K}) + r(1-\frac{n}{K})$$

For *f' (n) =0*, $-rn + r(K-n) = 0$

Thus $$n_{msy} = \frac{K}{2} \qquad 3.4$$

Hence $$f(\frac{K}{2}) = \frac{rK}{4}$$

Therefore, if the fish population is maintained at half its carrying capacity, the population growth is at a maximum, and the sustainable yield is greatest. This is called the Graham´s Theory of Sustainable Fishing (Weiss, 2009). Thus, maximum sustainable yield of a fish population is reached when the stock level (biomass) is exactly half of its carrying capacity, K, as shown in Figure 3.1.

There are two biological equilibria $n^* = 0 \quad and \quad n^* = K$. Any stock size above zero and below the carrying capacity, K will lead to positive growth and hence an increase in the stock. Any stock level above the carrying capacity will lead to excessive environmental resistance and hence to a decline in the stock.

3.1.1

An Example

The logistic model was applied to the natural growth of the halibut population in certain areas of the Pacific Ocean. The biomass n of the halibut population at time t was measured in kilograms. The parameters in the logistic equation were estimated to have the values r = 0.71/year and K = 80.5 × 10^6 kg. Given an initial population n_0 = 0.25K, the biomass 2 years later and the time τ for which $n(\tau)$ = 0.75K were found. It had the logistic curve below (Boyce and DiPrima, 2001).

The Growth of Halibut Population with Time

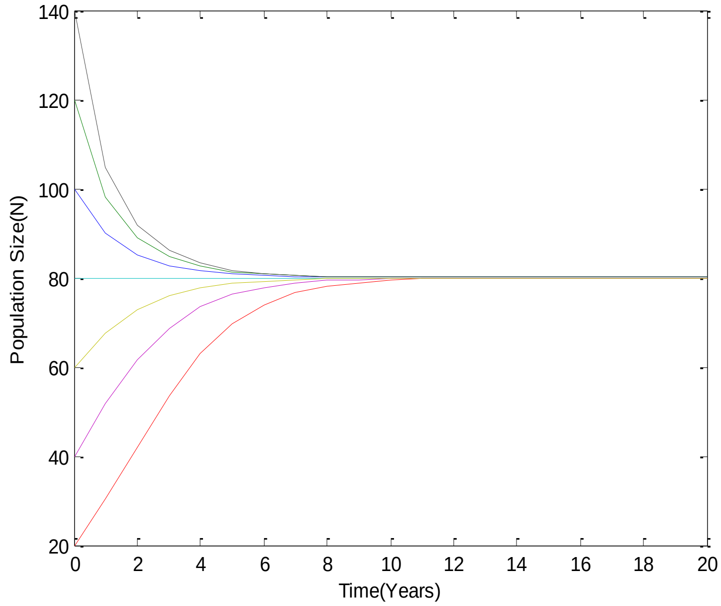

Figure 3.2. The population, n (X 10^6) Kilograms versus time,t years for population model of halibut in the Pacific Ocean.

The biomass of the fish population at any time t is given by Eq.(3.3)

$$n(t) = \frac{K}{1 + (\frac{K}{n_0} - 1)e^{-rt}}$$

Using the data given, it was found that

$$n(2) = \frac{K}{1 + (\frac{K}{0.25K} - 1)e^{-(0.71\times 2)}}$$

Simplifying further

$$n(2) = \frac{K}{1 + 3e^{-1.42}}$$

$K = 80.5 \times 10^6 Kg$, hence $n(2) \cong 46.7 \times 10^6 \ kg$.

To find τ. Eq.(3.3) was solved for t.

$$e^{rt} = \frac{n(1 - \frac{n_o}{K})}{n_o(1 - \frac{n}{K})}$$

Hence

$$t = \frac{1}{r}\ln\left[\frac{n(1-\frac{n_o}{K})}{n_o(1-\frac{n}{K})}\right] \qquad 3.5$$

Using the given values of *r*, n_o and *n*.τ was found to be

$$\tau = \frac{1}{0.71}\ln\left[\frac{0.75K(1-0.25)}{0.25K(1-0.75)}\right] = \frac{1}{0.71}\ln(9) \cong 3.095\ \textit{years}$$

3.2

The Growth Model with Harvesting Function

We now alter our viewpoint and consider the dynamical behavior of a fishery which is being harvested by fishermen. Harvesting is one of the most important parts of the fishery and it is frequently overlooked. It has a negative effect on the fish population. In the presence of harvesting, the loss rate due to harvesting, in general, depends both on the fishing effort and on the fish stock level. Therefore the inadequate understanding of the fishing behaviors of human being can contribute to fishery management failures (Levhari, D., Mirman L.J, 1980).

In the absence of harvesting, the natural growth of the fish population as a function of n is $f(n)$. Thus, the net growth of the fish population when harvesting activities are present is given by

$$\frac{dn}{dt} = f(n) - H(n) \qquad 3.6$$

When $f(n)>H(n)$, the net growth of the fish population is positive which means the population size is increasing. When $f(n)<H(n)$, the net growth of the population is negative. There is a decline in the population size. However, when $f(n)=H(n)$, the net growth is zero. There is no change in the population size and hence the population is at equilibrium.

$H(n)$ is the harvesting function or functional response. A functional response in ecology is the amount of resources captured per unit of time and per unit of predator, in fishery context, the amount of fish caught per unit of fishing effort (Auger, et al., 2009). The functional responses are generally classified into various types. The most common types are

- Constant or Quota harvesting.
- Holling´s Type I Function response
- Holling´s Type II Functional response
- Holling´s Type III Functional response.

Holling (1959) identified the three basic types of functional responses; Type I, II and III. Over the years, these models have become progressively simpler as the basic mechanisms have become better understood (Gotelli 2009, Wiess 2009).

3.3

Constant or Quota Harvesting

This illustrates the case where the fixed quantity of the fish is harvested every time. The number harvested, H does not depend on the quantity of fish present. Here Eq.(2.6) has the particular form;

$$\frac{dn}{dt} = rn(1-\frac{n}{K}) - H \qquad 3.7$$

The equilibrium satisfy

$$\begin{aligned}\frac{dn}{dt} &= f(n) - H = 0 \\ f(n) &= H \end{aligned} \qquad 3.8$$

We therefore have, $H = rn(1-\frac{n}{K})$

We solve Eq.(3.8) to find the population equilibrium. This represents sustainable yield. Geometrically, this can be found by plotting the line, H and the curve, $f(n)$ and finding where they intersect. The intersection points correspond to the equilibria for the system (see Figure 3.5). In the case of no harvesting i.e. $H = 0$, the species are in biological equilibrium. Eq.(3.6) then becomes Eq.(3.2) with

$n^* = 0$ *and* $n^* = K$. Any population size above 0 and below K, will lead to positive growth and hence increase in the stock.

3.3.1

Calculating Equilibrium points

We compute the equilibrium solutions of Eq (3.8). We have

$$rn - \frac{rn^2}{K} - H = 0$$

$$n^2 - Kn + \frac{KH}{r} = 0 \qquad 3.9$$

We find *n* by using quadratic formula

$$n_{1,2} = \frac{K}{2} \pm \frac{1}{2}\sqrt{K^2 - 4(\frac{KH}{r})} \qquad 3.10$$

If $K^2 - 4(\frac{KH}{r}) > 0$ then there are two distinct n-values, both of which are real numbers i.e.

$$n^*_1 = \frac{K}{2} - \frac{1}{2}\sqrt{K^2 - 4(\frac{KH}{r})} \quad and \quad n^*_2 = \frac{K}{2} + \frac{1}{2}\sqrt{K^2 - 4(\frac{KH}{r})}$$

If $K^2 - 4(\frac{KH}{r}) = 0$ then there is exactly one distinct real n-value, i.e. $n^* = \frac{K}{2}$

If $K^2 - 4(\frac{KH}{r}) < 0$ then there are *no* real roots.

3.3.2

Graphical Analysis

We use graphical analysis to study the behavior of the logistic curve with constant harvesting. We look at the three cases of constant harvesting.

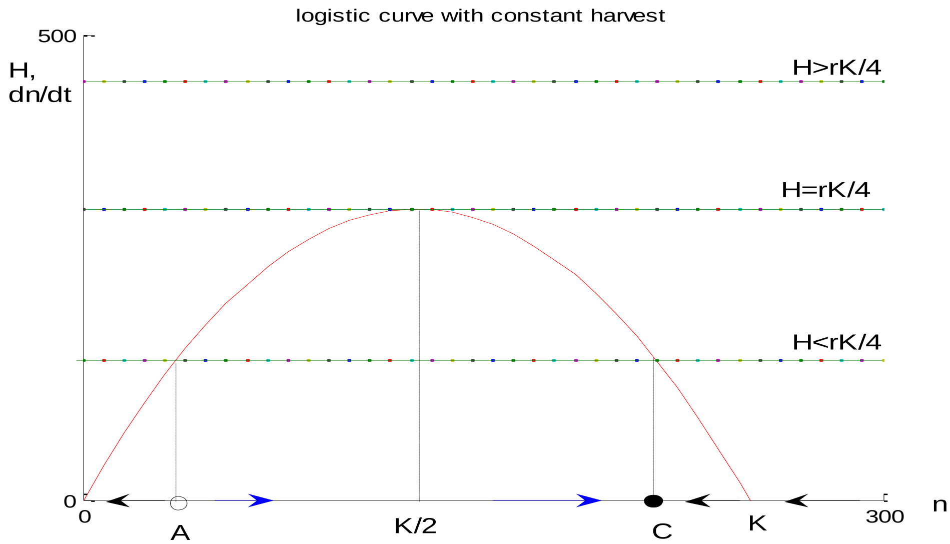

Figure 3.3. The rate of change of population, dn/dt is shown as a function of n. The curve is the natural growth rate. The horizontal lines are the loss due to harvesting (constant) at three different harvesting levels. Where the line lies above the curve; the net growth rate is negative. Where the line lies below the curve, the net growth rate is positive. The points of intersection correspond to possible equilibria.

At harvesting level H above $\frac{rK}{4}$, which is the maximum sustainable yield, the net growth of the population is negative since $f(n) << H$. What this means is that, the fish are being extracted faster than they can reproduce. The fish will accordingly be harvested to extinction.

At harvesting level H at the maximum sustainable yield, the population equilibrium is $n^* = \frac{K}{2}$. What this means is that, if the fish population begins at the carrying capacity, K then there will be no growth in the fish population but there will be harvesting equal to H_2, which will result in a decline in the fish stock because $f(n) < H$. When the fish population declines to half the carrying capacity then the natural growth in the fish population is matched by level of harvesting, and so this level of fish population can be sustained perpetually since $f(n) = H$. But the danger with this level is that, if the fish population should fall below the maximum sustainable yield, then the rate of harvesting will exceed the natural population growth i.e. $f(n) < H$, and there will be a decline in the fish population, the population approaches $-\infty$ and extinction will eventually result. Hence, the unique equilibrium $n^* = \frac{K}{2}$ of H_2 is half-stable.

Harvesting level H below the maximum sustainable yield, there are two possible population equilibria; $n_1^* = A \text{ and } n_2^* = C$ which have been found algebraically in the earlier section. When $0 < n < n_1^*$ then $f(n) < H$ and the population will decline to extinction. If $n_1^* < n < n_2^*$ then $f(n) > H$ and so the population will increase until n_2^* is reached. Finally, if $n > n_2^*$ again $f(n) < H$, so the population will decline until it reaches n_2^*. From the observation, we conclude that n_1^* is a locally unstable equilibrium and n_2^* is a stable equilibrium.

It is observed that when $H < \frac{rK}{4}$, two equilibria are created. As H increases, the equilibria move towards each other. As $H = \frac{rK}{4}$, the equilibria collide into a half-stable equilibrium at $n = \frac{K}{2}$, as soon as, $H > \frac{rK}{4}$ the equilibria annihilate as shown in Figure 3.3. Therefore a saddle-node bifurcation occurs at $H = \frac{rK}{4}$ corresponding to the equilibrium $n^* = \frac{K}{2}$.

Implication for the fishery

Brauer and Sanchez (1977) considered a lake with a certain fish species that was harvested to give a constant yield. Their analysis corresponds to Figure 3.3. In natural situations, it is observed that constant harvesting does not make sense biologically when the population is small (Weiss, 2009). For example, if there are only five tons of fish left in a certain area of the ocean, then harvesting ten tons per day makes no sense.

There is a danger in operating at the maximum sustainable yield because the unique equilibrium (i.e., half the carrying capacity, *K*) which is half-stable can easily tend the fishery to extinction. The fishery can however operate below the MSY, by keeping a higher fish stock but low harvesting activities hence low productivity.

Constant harvesting strategy was practiced by many fisheries in the past but it is no longer considered a safe management strategy.

3.4

Holling´s Type I Functional Response

This is also known as **Schaefer short term catch equation** in fisheries literature. Here, the rate of harvesting increases linearly with the fish population size. We assume the catch at time, t depends first on the population of fish available for catching, $n(t)$ and secondly, on the effort expended by the fishermen, $e(t)$. Effort in this sense is an index of all inputs commonly used for fishing - such as man-hours, trawlers, time spent at sea, nets, etc. We write this harvesting function as

$$H(n) = qen \qquad q > 0 \qquad 3.11$$

Where $\boldsymbol{q}$ denotes the technical efficiency (capturability) of the fishing fleet (Schaefer ,1957).

Eq.(3.6) now has the particular form,

$$\frac{dn}{dt} = rn(1 - \frac{n}{K}) - qen \qquad 3.12$$

3.4.1

Calculating Equilibrium Points

We compute the population equilibrium of Eq.(3.12)

$$f(n) = H(n) \qquad 3.13$$

$$rn(1 - \frac{n}{K}) = qen$$

The population equilibria are $n_1^* = 0$ and $n_2^* = K(1 - \frac{qe}{r})$.

If $r < qe$, $n_2^*<0$. If $r > qe$, $n_2^*>0$ and $r = qe$, when $n_2^*=0$.

3.4.2

Graphical Analysis

We perform a graphical analysis plotting the graphs of *f (n)* and *H(n)*. We look at the case where $r > qe$.

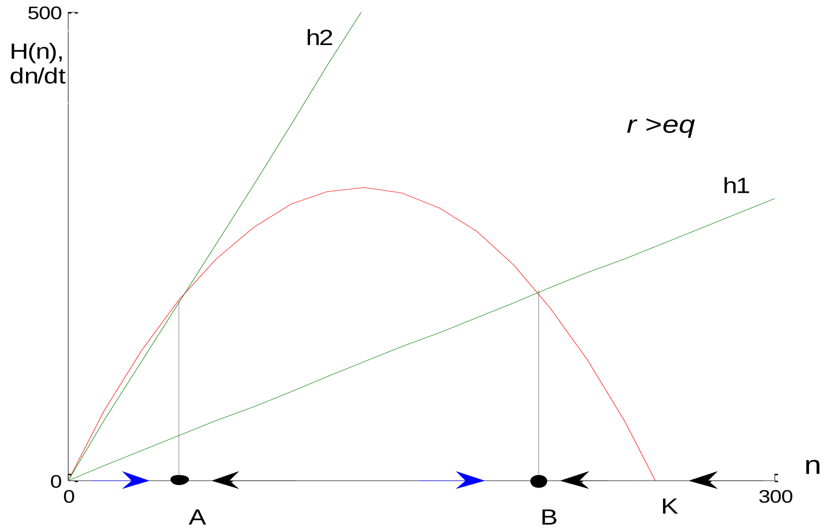

Figure 3.4. The rate of change of population, dn/dt is shown as a function of n. The curve is the natural growth rate. The lines are the loss due to harvesting at $h_1 = qe_1 n$ and $h_2 = qe_2 n$.

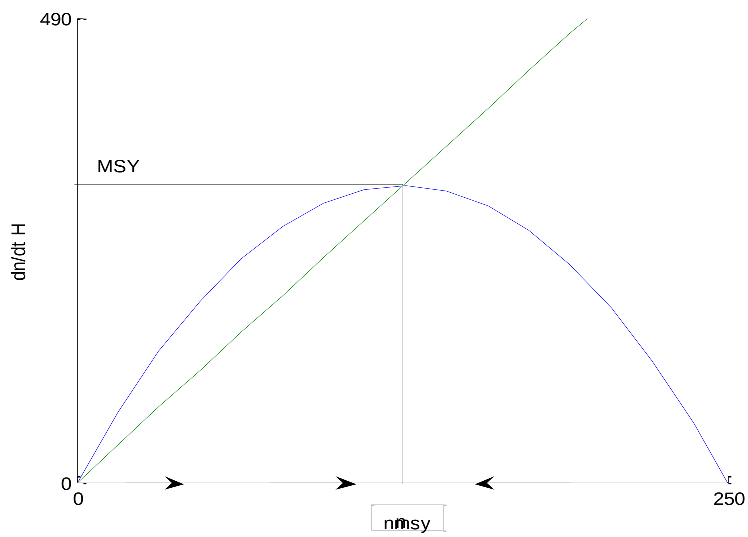

Figure 3.5. Harvesting at the maximum sustainable yield

For harvesting function h_1 , there are two population equilibria. That is, $n_1^*=0$ and $n_2^*=A$. When $n>0$, the net growth of the population is positive because $f(n) > H(n)$. Hence the population increases in size and grows away from zero. However, when population increases beyond the non-zero equilibrium A, the net growth in the population is negative because $f(n) < H(n)$; this results in a decline in the population size back to *A*. *A* is a locally stable equilibrium whiles $n=0$ is a locally unstable equilibrium.

When effort $e(t)$ is increased, the harvesting function h_1 moves to the left. This is represented by h_2. Still there are two equilbria just as in the case of h_1; the zero population and *B*. However, it is observed that $B<A$ as shown in Figure 3.4.

It is moticed that $n^*=0$ is always a population equilibrium. However it is stable when $r<qe$, half-stable when $r = qe$ and unstable when $r>qe$.

The non-zero equilibrium $n^* = K(1-\frac{qe}{r})$ on the other hand, is locally unstable when $r < qe$, disappears when $r = qe$ and locally stable when $r > qe$.

Hence the origin undergoes transcritical bifurcation as *r* is varied.

Implication for the fishery

From the analysis, it is noticed that when the fish population reproduces rapidly then the population will always grow away from the zero population irrespective of the initial population. However, increasing the effort extremely above the growth rate of the fish population draws the population to negative values and hence to extinction.

Harvesting can be done at the maximum sustainable yield without fear of extinction, because the non-zero equilibrium population is stable unlike the constant harvesting where the non-zero equilibrium population is half stable (see Figure 3.3 and Figure 3.5). Hence this harvesting strategy is preferred over the constant harvesting.

3.5

Holling´s Type II Functional Response

It is based on the assumption that the fishermen are limited by their capacity to hunt for the fishes. $H(n)$ increases with increasing fish population but at very high population, $H(n)$ saturates to some constant β, determined by the fishermen's harvesting capacity or processing rate. This behavior is modeled by the function

$$H(n) = \frac{\beta n}{n_H + n} \qquad 3.14$$

where β>*0* and $n_H > 0$.

This functional response is also used to model nutrient uptake –Monod response (Weiss, 2009) and chemical reactions- Michaelis-Merten response (Berryman, 2002).

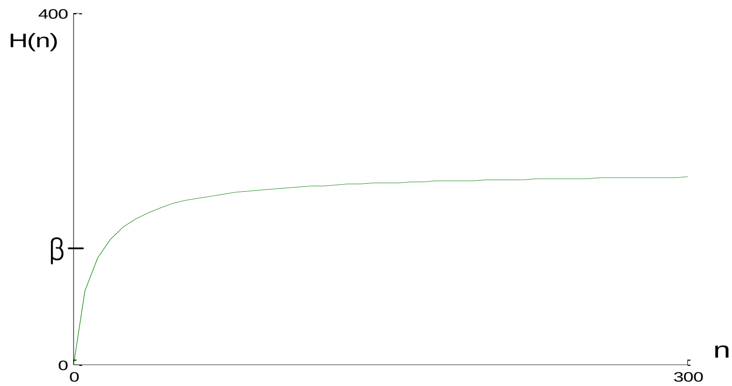

Figure 3.6. Holling´s Type II Frunctional response

Eq.(3.6) now has the particular form,

$$\frac{dn}{dt} = rn(1-\frac{n}{K}) - \frac{\beta n}{n_H + n} \qquad 3.15$$

There are four parameters: r, K, β, n_H so we reduce the number of parameters, to simplify the analysis. This is done by introducing rescaled variables. This process is known as nondimensionalizing the system. For an actual discussion of this process see Strogatz (1994).

Both n_H and *K* have the same dimension as *n* and so either n/n_H or *n/K* could serve as a dimensionless population level. We let

$$x = \frac{n}{K},\ \tau = rt,\ a = \frac{n_H}{K},\ \text{and } h = \frac{\beta}{rK}$$

Then Eq.(3.15) becomes,

$$\frac{dx}{d\tau} = x(1-x) - h\frac{x}{a+x} \qquad 3.16$$

where h>*0* and *a*>*0*

3.5.1

Calculating Equilibrium Points

$$\frac{dx}{d\tau} = x(1-x) - h\frac{x}{a+x}$$

We have
$$\frac{dx}{d\tau} = 0$$
$$\Rightarrow x(1-x) = h\frac{x}{(a+x)}$$

We get *x*=0* and *(1-x) =h/(a+x)*, whose roots give the two additional equilibria.

$$for\ x^* = 0,$$
$$f'\left(x^*\right) = a - h \qquad 3.17$$

When $h<a$, we get $f'(x^*)>0$, $x^*=0$ is a repeller

When $h>a$, we get $f'(x^*) <0$, $x^*= 0$ is an attractor

Hence $x^*=0$ undergoes a transcritical bifurcation when $h=a$.

We find the roots of $(1\text{-}x) = h/(a+x)$

$$(1-x) = \frac{h}{(a+x)}$$
$$(1-x)(a+x) - h = 0$$
$$a + x - ax - x^2 - h = 0$$
$$x^2 - (1-a)x + (h-a) = 0$$

We have a quadratic equation whose roots are given by

$$x_{1.2} = \frac{1}{2}((1-a) \pm \sqrt{(1-a)^2 - 4(h-a)} \qquad 3.18$$

We can have one, two values or no value at all for x depending on the value of the discriminant, $\Delta = (1-a)^2 - 4(h-a) = (1+a)^2 - 4h$. Therefore a bifurcation occurs when $h = \frac{(1+a)^2}{4}$.

3.5.2

Graphical Analysis

Using graphical analysis, we study the behaviour of the equilibria as h is varied from $h_1 = a$ to $h_2 = \frac{1}{4}(1+a)^2$.

1. For $h<a$, there are two roots with opposite signs.

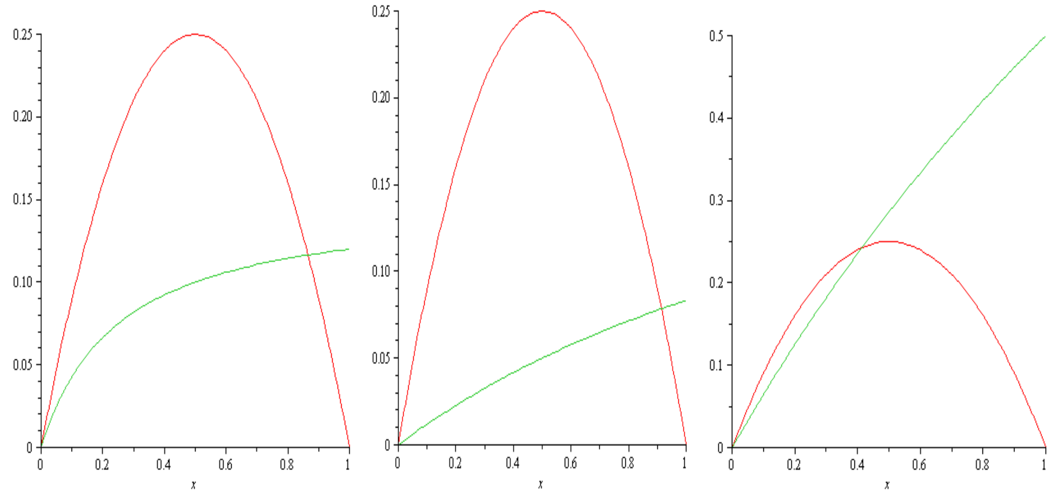

Figure 3.7. The parabola represents *f(x)* and the other curve represents *h(x)*. The points of intersection correspond to the possible equilibria. Where the parabola is above the curve, the net growth rate is positive (*f(x)* >*h(x)*) and the flow along the x-axis is to the right. Where the curve is above the parabola, the net growth rate is negative (*f(x)*<*h(x)*) and the flow along the x-axis is to the left. (1) *h*=0.15 and *a*=0.25 (2) *h*=0.25and *a*=2 (3) *h*=2 and *a*=3 respectively.

2. If $h = a$ then at least one *x*-value is zero. The other value can be negative or positive.

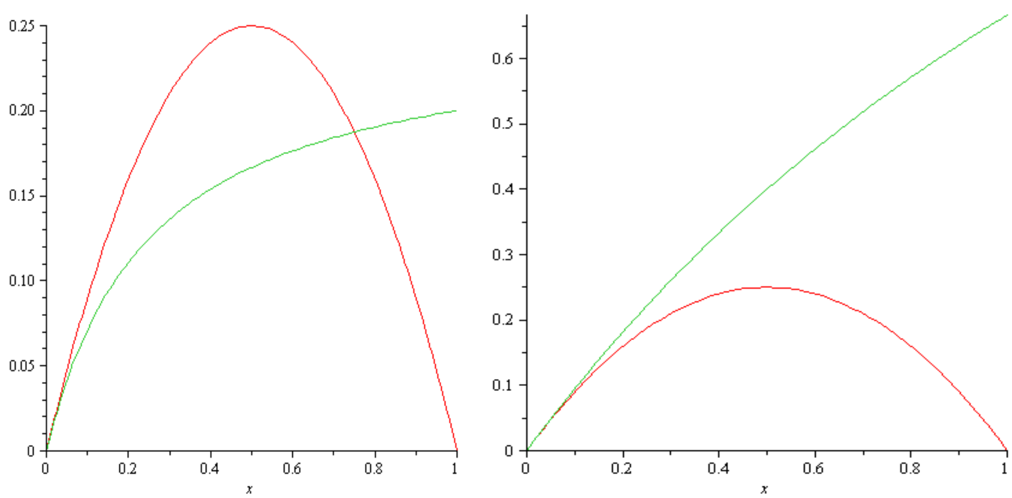

Figure 3.8. *f(x)* and *h(x)* against *x*. (1) *h*=0.25 and *a*=0.25 (2) *h*=2 and *a*=2 respectively.

3. When $a < h < \frac{(1+a)^2}{4}$ there are 2 roots with the same sign. For a<1 the roots are positive and for *a>1* the roots are negative.

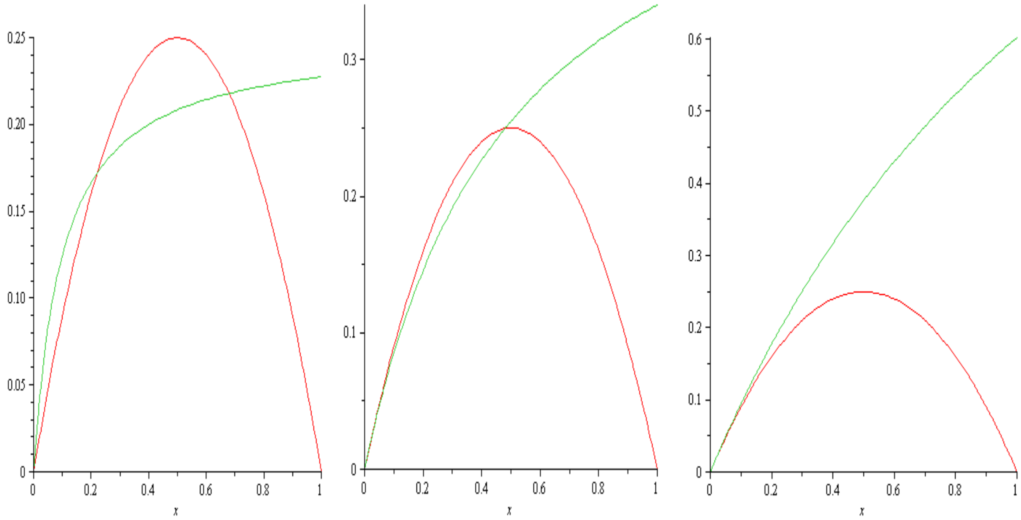

Figure 3.9. *f(x)* and *h(x)* against *x*. (1) *h*=0.25 and *a*=0.1 (2) *h*=0.51 and *a*=0.50 (3) *h*=2.05 and *a*=2 respectively.

4. $h = \dfrac{(1+a)^2}{4}$, there is at least one root equal to zero and a positive root if a<1.

For a>1, we have $x = 1-a \pm (1-a) = \begin{cases} 1-a-(1-a)=0 \\ 1-a+(1-a)=2(1-a)<0 \end{cases}$

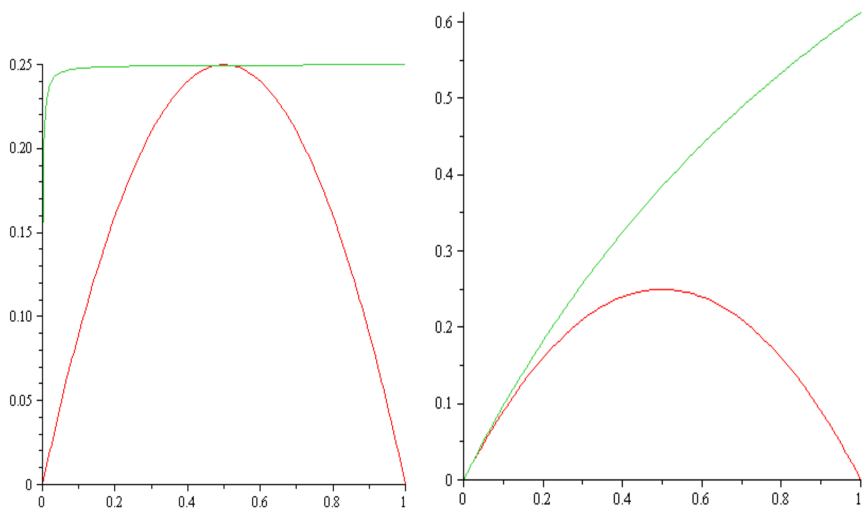

Figure 3.10. *f(x)* and *h(x)* against *x*. (1) *h*=0.25 and *a*= 0.001. (2) *h*=1.5 and *a*=1.45.

5. If $a < \frac{1}{4}(1+a)^2 < h$ there are complex *x*-values.

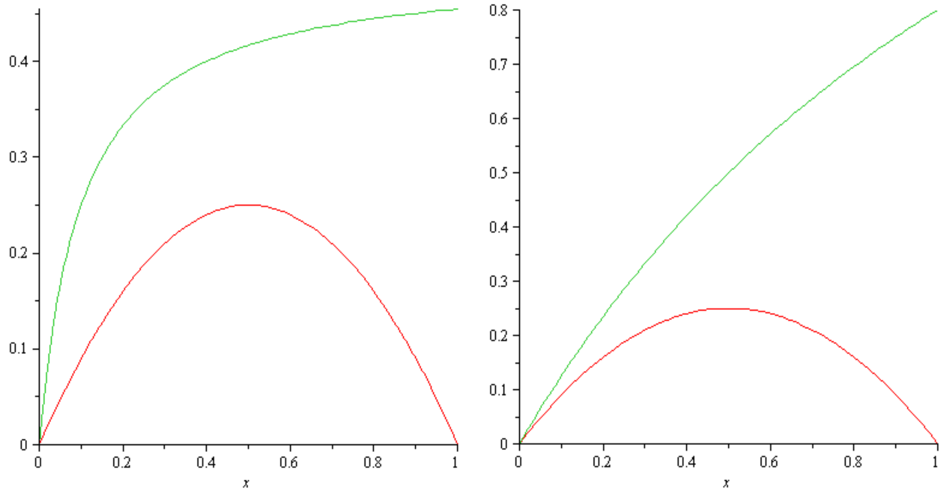

Figure 3.11. *f(x)* and *h(x)* against *x*. The green curve represents *h(x)* and the red curve represents *f(x)*. (1) h=0.5 and a=0.1 (2) h=2 and a=1.5 respectively.

It is observed that $x^*=0$ is always an equilibrium. However, it changes its stability as h is varied.

For values of $h<h_1$, there are two equilibria, a stable positive equilibrium and an unstable equilibrium at the origin. For $a<1$ the stable equilibrium is bigger than when $a>1$ as shown in Figure 3.7.

For values of $h>h_2$, there is a unique equilibrium $x^*=0$, which is a stable equilibrium for both $a<1$ and $a>1$ as shown in Figure 3.11.

For values of $h_1< h<h_2$, there are three equilibria for $a<1$; two stable equilibria, $x^*=0$ and a positive value, whose domain of attraction is divided by an unstable equilibrium but for $a>1$, there is a unique stable equilibrium $x^*=0$ as shown in Figure 3.9.

The two positive equilibria created when $h_1< h<h_2$ *and* $a<1$, approach each other, coalesce and create a new equilibrium when $h=h_2$. For $a>1$, the origin is the unique stable point as shown in Figure 3.10.

As h increases above h_2, there is a unique equilibrium which is the origin for both $a<1$ and $a>1$, all other equilibria disappear as shown in Figure 3.11.

Implication for the fishery

From the analysis, it is observed that when $a>1$, the harvesting rate is extremely higher than the natural growth function and harvesting saturates at a population size above the carrying capacity of the population. The possible population equilibrium for most levels of harvesting are negative which means extinction. Therefore for sustainable fishery $\boldsymbol{a = n_H/K}$ should be maintained at a value less than 1.

When $h<h_1$, harvesting activities are less because the fish population is small. This allows the fish population to increase until it reaches the stable equilibrium, which in this case is slightly below the fish population's carrying capacity. Harvesting activities within the region h_1 and h_2 will cause the fish population to tend towards either the stable equilibrium or towards the zero population depending on the initial population. For any initial population greater than the unstable equilibrium, that population will increase until it reaches the stable equilibrium. On the other hand, any initial population smaller than the unstable equilibrium will tend to decrease until it becomes zero i.e. the population will be heading for extinction.

When $h> h_2$, harvesting activities are very intense and $f(n) << H(n)$. The net growth rate of the population is negative and so the population will be reducing at a faster rate until it reaches extinction (zero population). Here the origin is the unique stable equilibrium.

As shown in Figure 3.10, when the harvesting function saturates at the maximum sustainable yield (MSY), the population will move towards extinction since the positive equilibrium is half-stable and the stable equilibrium is the origin.

3.6

Holling´s Type III Functional Response

Type III functional response is similar to Type II in that at high levels of fish population, saturation occurs. There is almost no harvesting when fish are scarce; the fishermen seek food elsewhere. However, once the population exceeds a certain critical level $n = n_H$, the harvesting turns on sharply (faster than linearly) and then saturates (the fishermen are catching as much as they can).

$$H(n) = \frac{\beta n^2}{{n_H}^2 + n^2} \qquad n_H, \beta > 0 \qquad 3.19$$

From the equation, we observe that as $n \to \infty$, $H(n) \to \beta$ and as $n \to 0$, $H(n) \to 0$. When $n = n_H$, $H(n) = \frac{\beta}{2}$, exactly half its maximum.

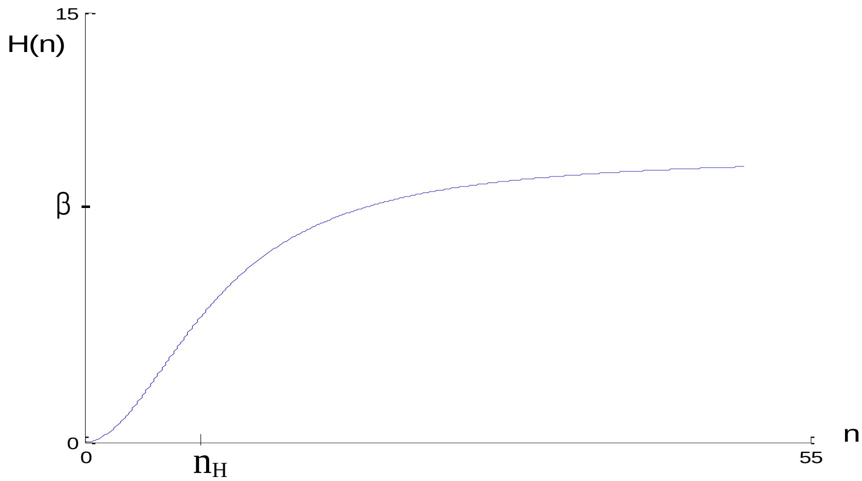

Figure 3.12 Hollings´s Type III functional response.

Notice that *H´(0)=0*.

Eq.(3.6) has the particular form;

$$\frac{dn}{dt} = rn(1-\frac{n}{K}) - \frac{\beta n^2}{n_H{}^2 + n^2} \qquad 3.20$$

Now the origin will be always a unstable, since *f' (0)>H' (0).*

3.6.1

Calculating Equilibrium points

To analyze the equilibria we write the equation in dimensionless form by using $x = \frac{n}{n_H}$, $\tau = \frac{\beta t}{n_H}$, $R = \frac{rn_H}{\beta}$, and $k = \frac{K}{n_H}$.

Then Eq.(3.20) becomes,

$$\frac{dx}{d\tau} = Rx(1-\frac{x}{k}) - \frac{x^2}{1+x^2} \qquad 3.21$$

which is our final dimensionless form. Here R and k are the dimensionless growth rate and carrying capacity respectively.

Eq.(3.21) has an equilibrium at $x^* = 0$. The other equilibria are given by the roots of Eq.(3.22) .

$$R(1-\frac{x}{k}) = \frac{x}{1+x^2} \qquad 3.22$$

Algebraically, the stability of the equilibria of Eq.(3.22) can be classified using the discriminant of the cubic equation. However this can be tedious. We proceed using graphical analysis.

3.6.2

Graphical Analysis

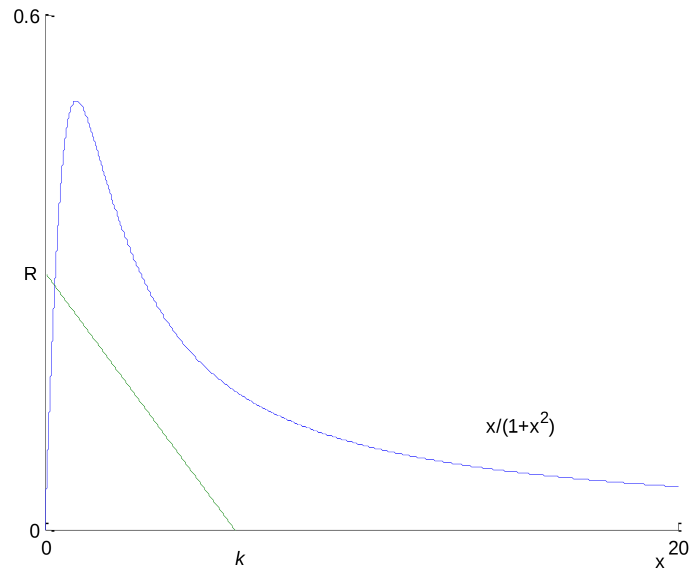

Figure 3.13 Graph of dx/dτ versus x for sufficiently small k and R

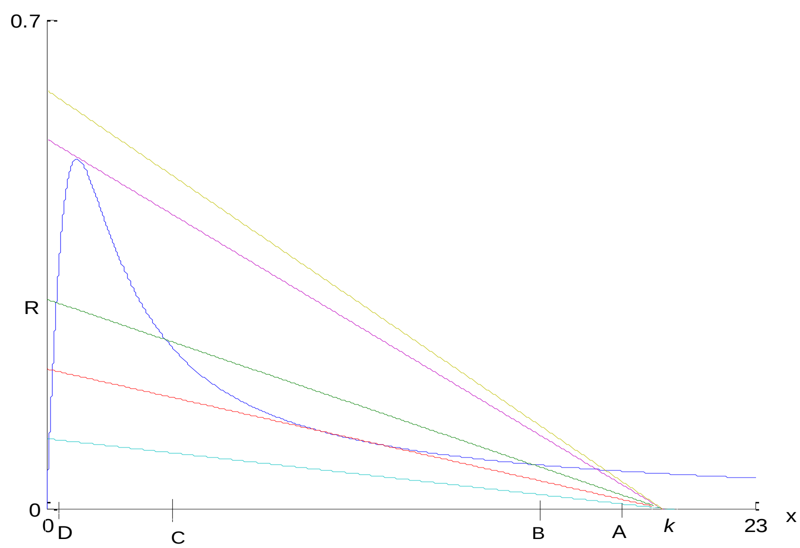

Figure 3.14 Graph of dx/dτ versus x for k, sufficiently large.

Graphing the right- and left- hand sides of Eq.(3.22) it is observed that as we vary the parameters *R* and *k*, the line moves but the curve does not. Figure 3.13 shows that if *k and R* are sufficiently small, there is exactly one intersection. However, for large *k*, we can have one, two, or three intersections depending on the value of *R* (see Figure 3.14).

Let's suppose that there are three intersections which project on x-axis in points B, C and D (third line in Figure 3.14). As we decrease *R* with *k* fixed, the line rotates counter-clockwise about the point *(k,0)* .Then points *B* and *C* approach each other and eventually coalesce in a saddle- node bifurcation when the line intersects the curve tangentially (second line from below in Figure 3.14**)**. After the bifurcation, the only remaining equilibrium is *D* (in addition to $x^*=0$). Similarly, *D* and *C* can collide and annihilate as *R* increased (fourth line from below in Figure 3.14).

It is easy to determine the stability of the equilibria, since Eq.(3.21) is positive where the line is above the curve and is negative where it is below, so, we observe that the stability type alternates as we move along the x-axis. We recall that $x^*=0$ is always unstable.

For relatively large values of *R*, point A slightly to the left of *(k,0)* is a stable equilibrium(in addition to the origin which is an unstable equilibrium) as shown in Figure 3.15.

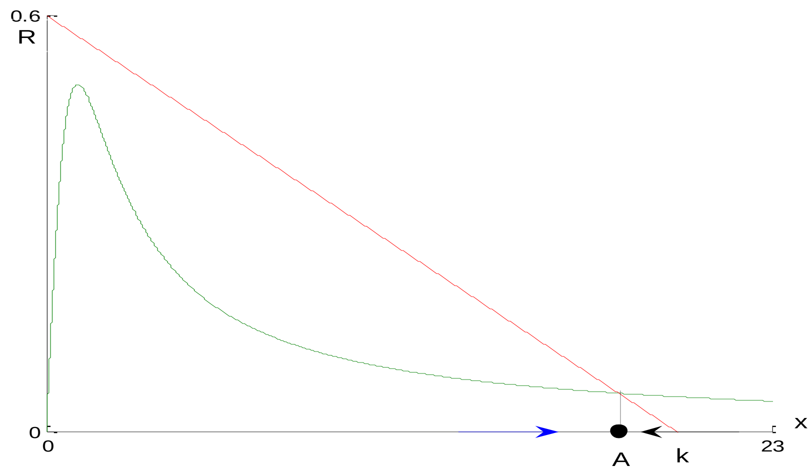

Figure 3.15

For small values of *R*, point E slightly to the right of (0,0) is a stable equilibrium (in addition to the origin is an unstable equilibrium) as shown in Figure 3.16.

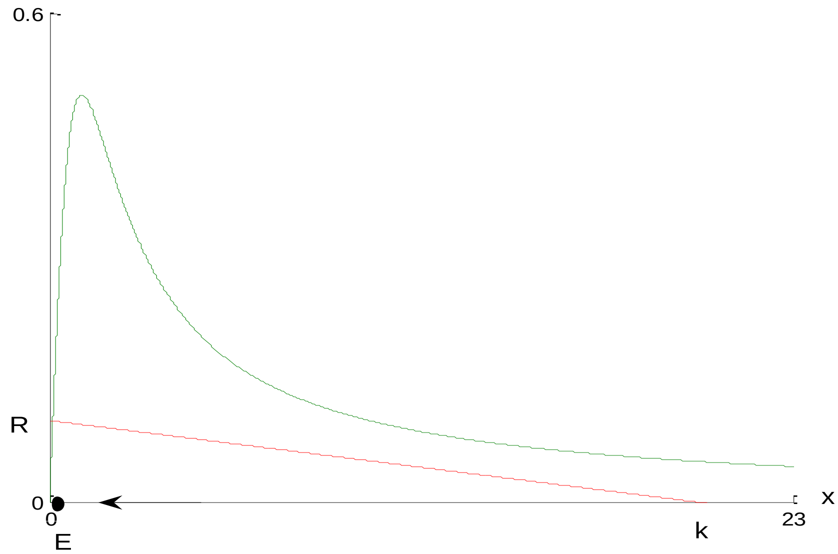

Figure 3.16

For intermediate values of *R*, there are four equilibria. The points B and D correspond to two stable equilibria whose domain of attraction is divided by the unstable equilibrium corresponding to C (in addition to the origin which is unstable) as shown in Figure 3.17.

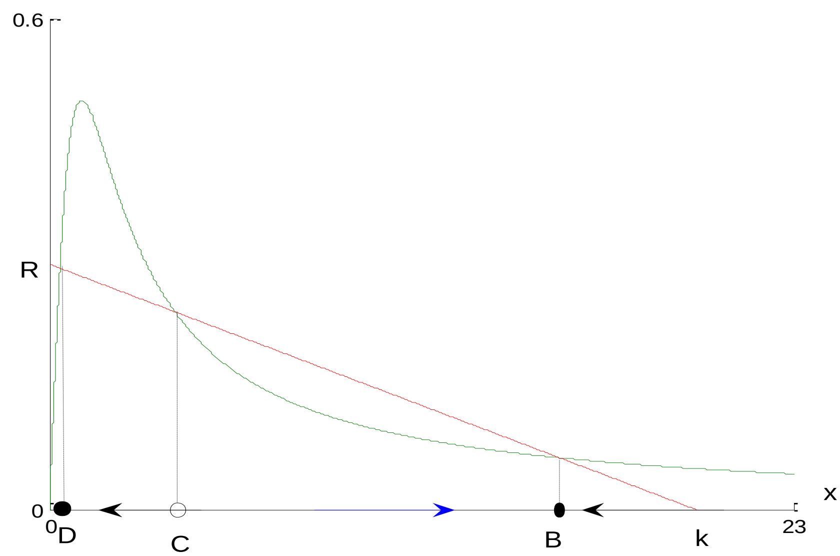

Figure 3.17

In the case of two stable equilibria, the behavior of the system is determined by the initial condition x_0: if $x_o>C$ then x will move towards B. if $x_o<C$ then it will

move towards D. In this sense, the unstable equilibrium C plays the role of a threshold.

Implication for the fishery

From the analysis, the dynamics of Type III response function are quite similar to Type II. However, one obvious difference is that, the stability of the origin in Type II changes whiles the origin is always unstable in Type III. That is, the population never goes extinct (no matter the initial population) because harvesting activities reduce extremely or cease when the fish population is small. This permits the population to increase exponentially away from zero.

For stocking densities in the intermediate regions, we have two alternate stable states. Thus the population will tend toward either the upper or the lower equilibrium value (non-zero) depending on the initial population; for initial population greater than the breakpoint *C*, the population will increase to the higher population *B* and initial population smaller than *C* will decrease/increase to the lower population *D.*

Just as in Type II, there is danger in operating above the maximum sustainable yield. Any misjudgment can push the fishery to collapse although not to extinction but a very low population (Figure 3.16)

The essential feature that leads to two alternative stable states is the assumption that $k=K/n_H$ is significantly large. That is the population has a large carrying capacity *K*.

Further discussion of Type III functional response can be found in Ludwig et al (1978), May (1977) and Noir- Mey (1974).