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B S Goh
Curtin University Malaysia

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SOME STABILITY CONDITIONS FOR DISCRETE-TIME SINGLE SPECIES MODELS

■ M. E. FISHER and B. S. GOH
Mathematics Department,
University of Western Australia,
Nedlands, W.A. 6009,
Australia

■ T. L. VINCENT
Aerospace and Mechanical Engineering Department,
University of Arizona,
Tucson, Arizona, 85721, U.S.A.

Standard results relating to the stability of autonomous first order difference equations are restated here with slight modifications so as to apply directly to equations in which the state variable remains positive. Some simple and effective tests for both local and global stability of these first order difference equations are presented. The main results are illustrated with examples drawn from population biology.

1. Introduction. There are many instances when a situation can be approximately modelled by a first order difference equation. This is one of the reasons for the increase in the number of studies made of these equations in recent times. May (1974), for example, has shown that the very simplest nonlinear difference equation can exhibit a very complex range of behaviour. The standard method for the stability analysis of these equations usually consists of a linearised analysis to determine stability relative to small perturbations of the initial state from the equilibrium. This restriction to small perturbations means that the analysis may be of limited practical use. For practical stability a far more powerful tool is the Liapunov function, the use of which has increased dramatically in the study of dynamical systems since the 1950's even though the "second method" of Liapunov was originally published in 1892 (Liapunov, 1892).

In this paper we are concerned solely with the stability of nonlinear, autonomous first order difference equations of the general form

$$x_{n+1} = F(x_n), \quad n = 0, 1, 2, \ldots, \tag{1}$$

where x_n is positive for all n, and F is a continuous function except where otherwise indicated in the text. We shall now provide an explanation of the terms local stability and global stability as used in the context of this paper. An equilibrium x^* of (1) satisfying $F(x^*) = x^*$ is said to be: *stable* (or *locally stable*) if, when the system experiences a slight perturbation from its equilibrium, all subsequent motions remain in a correspondingly small neighbourhood of the equilibrium (more precisely, for every neighbourhood U of x^* there exists a neighbourhood V of x^* such that $x_n \in U$ for $n = 1, 2, 3, \ldots$ whenever $x_0 \in V$); an *attractor* (or *local attractor*) if there is a neighbourhood U of x^* such that $x_n \to x^*$ as $n \to \infty$ whenever $x_0 \in U$; a *global attractor* if $x_n \to x^*$ as $n \to \infty$ for all $x_0 > 0$; *globally stable* if it is stable and a global attractor.

In what follows the basic equation (1) will be thought of as a single species population model with x_n being the magnitude of the population in the nth generation. Clearly however there are many other situations outside population biology where (1) applies and the results obtained in this paper will be equally applicable in these situations. For example x_n may represent the price level of a commodity in an economic model or, in epidemiology, x_n may represent the number of infectives in a population at a given time.

Two theorems relating to the stability of (1) are presented in Section 2 of this paper. The first is simply a restatement of a well known global stability result based on the "second method" of Liapunov. The hypothesis of this theorem is then modified slightly in the second theorem.

The remainder of the paper describes some simple and effective tests for both local and global stability. These tests are based upon the concepts of Liapunov functions and simple geometrical ideas. The main results are illustrated with examples drawn from population biology.

2. *Two Stability Theorems.*

Suppose that (1) represents a model of a population with non-overlapping generations which has a non-trivial equilibrium at x^* where $F(x^*) = x^*$. Some of the more popular functional forms which have been employed in ecological models of this type are depicted in Table I.

Two results which will prove to be useful later are now given in the following two theorems. The first of these is simply a direct translation of a well known result on stability by means of Liapunov's "second method". If we modify the standard Liapunov theorem for global stability (Corollary 1.2* of Kalman and Bertram, 1960) we obtain

TABLE I
Some Difference Equations, Taken From the Biological Literature

$F(x)$	Reference
$x[1+r(1-x/K)]$	Maynard Smith (1968)
$x\exp[r(1-x/K)]$	Ricker (1954)
$\lambda x[1+ax]^{-b}$	Hassell (1974)
$x[1/(b+cx)-\sigma]$	Utida (1957)
$\lambda x[1+(\lambda-1)(x/K)^c]^{-1}$	Maynard Smith (1974)

THEOREM 1. *Let V be a continuous function and $\Delta V(x)=V(F(x))-V(x)$. The equilibrium x^* of* (1) *is globally stable if:*

(a) $V(x)>0$ *for all* $x>0$, $x\neq x^*$ *and* $V(x^*)=0$;
(b) $\Delta V(x)<0$ *for all* $x>0$, $x\neq x^*$;
(c) $V(x)\to\infty$ *monotonically as* $x\to\infty$;
(d) $V(x)\to\infty$ *monotonically as* $x\to 0+$.

The proof of this theorem follows directly from that of the standard theorem (Kalman and Bertram, 1960) upon applying the transformation $y=\log(x/x^*)$ which maps $(0,\infty)$ onto the whole of the real line. The use of this theorem is illustrated in the following example.

Example 1. Consider the second equation in Table I, i.e.

$$x_{n+1}=x_n\exp[r(1-x_n/K)], \tag{2}$$

considered by some to be the difference analogue to the logistic differential equation. The equilibrium point is at $x^*=K$, the carrying capacity. Let

$$V(x)=\tfrac{1}{2}(x^2-K^2)-K^2\log(x/K).$$

Then V satisfies conditions (a), (c) and (d) of Theorem 1. Also it can be shown (Goh, 1977) that for $r\in(0,2)$, $\Delta V(x)<0$ for all $x>0, x\neq K$. Hence, for these values of $r, x^*=K$ is globally stable.

The hypothesis of Theorem 1 can be modified slightly by removing condition (d) and imposing a positivity condition on the function F in (1).

THEOREM 2. *Let V be a continuous function. The equilibrium x^* of* (1) *is globally stable if*

(a) $V(x)>0$ *for all* $x>0$, $x \neq x^*$ *and* $V(x^*)=0$;
(b) $\Delta V(x)<0$ *for all* $x>0$, $x \neq x^*$;
(c) $V(x) \to \infty$ *monotonically as* $x \to \infty$;
(d) $F(x)>0$ *for all* $x>0$.

Proof. Since $F(x)>0$ for all $x>0$, we have that any solution of (1) which begins in $(0, \infty)$ must remain there. Also $\Delta V(x)<0$ for all $x>0$ implies that all bounded solutions of (1) tend to x^* as $n \to \infty$. But conditions (b) and (c) imply that all solutions are bounded. Hence every solution which begins in $(0, \infty)$ remains there and approaches x^* as $n \to \infty$.

Example 2. Consider again the model described by (2). It has been suggested (May, 1974) that a suitable Liapunov function for this model is given by $V(x)=(x-K)^2$. We see that V satisfies conditions (a) and (c) of Theorem 2. Also for $0<r<2$, it can be shown (see Appendix) that $\Delta V(x)<0$ for all $x>0$, $x \neq K$. Hence the equilibrium point $x^*=K$ is globally stable since $F(x)>0$ for all $x>0$.

3. Simple Stability Tests Based on Liapunov Functions. For many population models it may be difficult or even impossible to show analytically, for a given V function, that $\Delta V(x)<0$ for all $x>0, x \neq x^*$. We can however obtain some simple quantitative tests for both local and global stability based on the concept of a Liapunov function. For (1) consider the function

$$V(x)=[\log(x/x^*)]^2 \tag{3}$$

as a possible candidate for a Liapunov function. V satisfies conditions (a), (b) and (d) of Theorem 1 and

$$\Delta V(x)=[\log(F(x)/x^*)]^2-[\log(x/x^*)]^2.$$

Since the difference between the squares of two numbers can be written as the product of the sum of the two numbers and their difference, it follows that

$$\Delta V(x)=\log(xF(x)/x^{*2}) \, . \log(F(x)/x).$$

Hence we have that $\Delta V(x)<0$ if and only if

(i) $x<F(x)<x^{*2}/x$ for all $x \in (0, x^*)$;
(ii) $x^{*2}/x<F(x)<x$ for all $x \in (x^*, \infty)$.

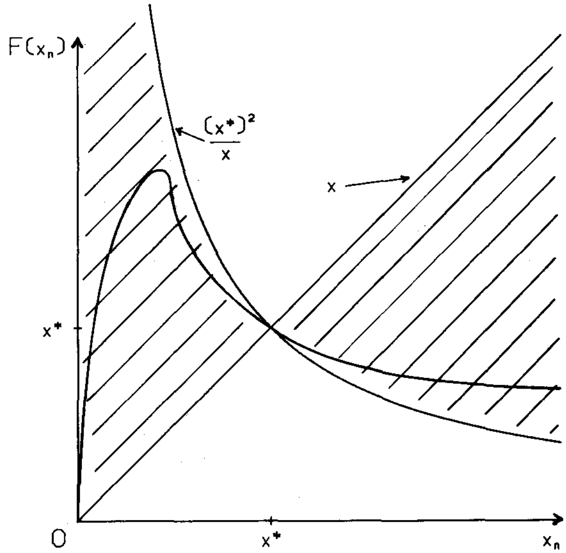

Figure 1. Equation (1) is globally stable if $F(x)$ lies inside the shaded region

These inequalities are illustrated in Figure 1. We see that if the graph of $F(x)$ lies inside the shaded region in Figure 1 then the equilibrium point x^* is globally stable. A function which satisfies these conditions is illustrated. In the case when the graph of $F(x)$ crosses the boundary of the shaded region a region of attraction for the model can be obtained. For example, if $F(x)$ crosses the boundary at $x=a$, then a region of attraction for the model is given by the open interval $A=\{x>0\backslash V(x)<V(a)\}$. This is illustrated in Figure 2.

If $F(x)$ tends to zero faster than x^{*2}/x as x tends to infinity then the V function given in (3) is obviously unsuitable for displaying global stability. An example of this type of function is given by (2) which has been shown to be globally stable for $0<r<2$. Here $F(x)$ behaves like $x\exp(-rx/K)$ for x large. To accommodate functions of this type we can modify V of (3) to the form

$$V(x)=c_1[(x^p-x^{*p})/p-x^{*p}\log(x/x^*)]+c_2[\log(x/x^*)]^2,$$

where $c_1\geqq 0, c_2\geqq 0$ and $p>0$. This leads to

$$\Delta V(x)=c_1[(F^p(x)-x^p)/p-x^{*p}\log(F(x)/x)]$$
$$+c_2\{[\log(F(x)/x^*)]^2-[\log(x/x^*)]^2\}.$$

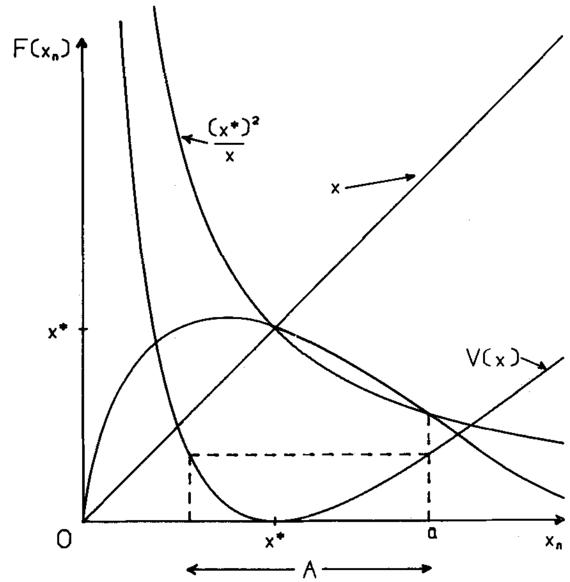

Figure 2. A region of attraction for the function displayed is given by the interval A

Once again the equation $\Delta V(x)=0$ defines exactly two functions of x, one of which is given by $F(x)=x$ as before. The other function, say G, has to be determined numerically (a simple root finding method will suffice). So we have the result that $\Delta V(x)<0$ if and only if there exists non-negative constants c_1 and c_2 and a positive constant p such that

(i) $x<F(x)<G(x)$ for all $x\in(0,x^*)$;
(ii) $G(x)<F(x)<x$ for all $x\in(x^*,\infty)$.

It is easy to show that for $c_2\neq 0$,

$$G(x)\sim\exp\left[-\left(\frac{c_1x^p}{c_2p}\right)^{\frac{1}{2}}\right]$$

as x tends to infinity. Hence to illustrate that (2) is globally stable we would need to choose $p\geqq 2$ in order to ensure that the inequality $F(x)>G(x)$ is satisfied for x large. If $c_2=0$, then

$$G(x)\sim\exp\left[-\frac{1}{p}(x/x^*)^p\right]$$

as x tends to infinity and p would now need to be $\geqq 1$. Figure 3 depicts graphs of $G(x)$ for various choices of c_1, c_2 and p.

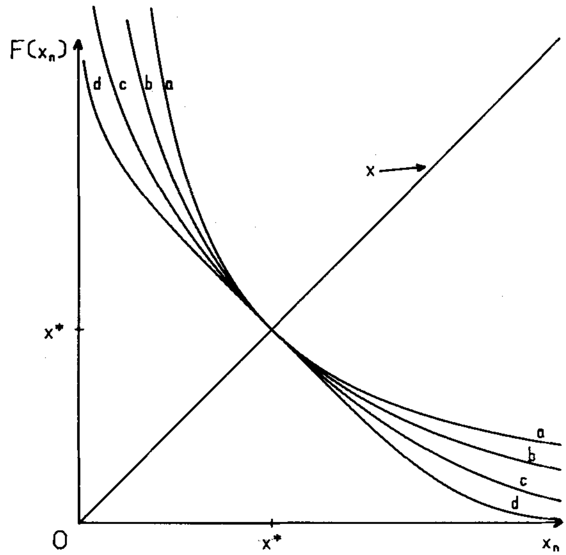

Figure 3. Sketches of $G(x)$ for the cases (a) $c_1=0$, $c_2=1$; (b) $c_1=1$, $c_2=1$, $p=2$; (c) $c_1=1$, $c_2=0$, $p=2$ and (d) $c_1=1$, $c_2=0$, $p=3$

4. A Geometric Approach. In the previous section stability regions were obtained by examining the equation $\Delta V(x)=0$ for a particular Liapunov function V. We now employ a purely geometric approach to obtain a different class of stability regions.

Take any point on the line $F(x)=x$ lying between the origin and the point corresponding to equilibrium. From this point construct a square, which contains the equilibrium point, with sides parallel to the axes as shown in Figure 4. Draw lines from the equilibrium point through the vertices P and Q of this square. Clearly, if the plot of $F(x)$ of (1) corresponded to the lines just drawn, then (1) would be neutrally stable. This follows by construction since for any x_n,

$$x_{n+1}=F(x_n)$$

$$x_{n+2}=F(x_{n+1})=x_n.$$

That is, the system returns to x_n after every two time steps. These lines then correspond to neutral stability. We will now show that x^* of (1) will be globally stable if the graph of $F(x)$ lies completely in the regions bounded by the two lines and the line $F(x)=x$ (see Figure 4). By varying the initial point on the line $F(x)=x$ and the side length of the square we can obtain an infinite variety of stability regions. In fact the lines through P and Q can be characterised purely in terms of their slope. If we define

$R(x)$ as the equation of the line through P and $S(x)$ as the equation of the line through Q, then

$$R(x)=x^*+(x^*-x)\tan\theta,$$
$$S(x)=x^*-(x-x^*)\cot\theta, \tag{4}$$

where θ is the angle shown in Figure 4. For $0<\theta<\pi/2$ we have the important property that

$$S(R(x))=R(S(x))=x.$$

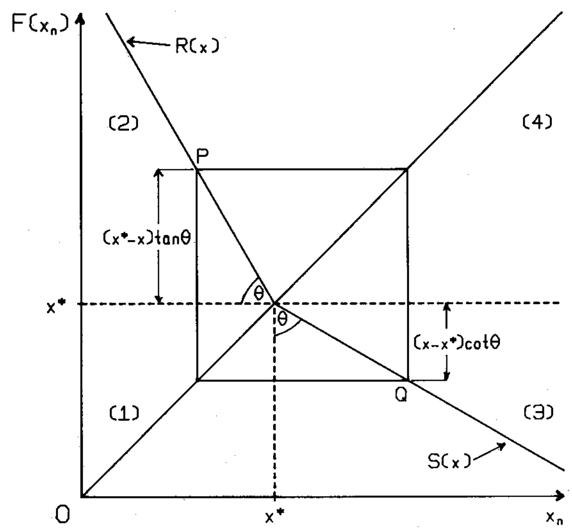

Figure 4. Equation (1) is globally stable if $F(x)$ lies in the region bounded by the lines $R(x)$, $S(x)$ and x

This construction can now be formalised in the following theorem.

THEOREM 3. *The equilibrium point* x^* *of* (1) *is globally stable if there exists a* $\theta\in(0,\pi/2)$ *such that*

(a) $x<F(x)<R(x)$ *for all* $x\in(0,x^*)$;
(b) $\text{Max}(0,S(x))<F(x)<x$ *for all* $x\in(x^*,\infty)$;

with $R(x)$ *and* $S(x)$ *defined by* (4).

Proof. We shall show that a Liapunov function for (1) is

$$V(x)=\begin{cases}R(x)-x & \text{if} \quad x\in(0,x^*],\\ x-S(x) & \text{if} \quad x\in(x^*,\infty).\end{cases}$$

V satisfies conditions (a) and (c) of Theorem 2 and F satisfies condition (d) of Theorem 2. The proof is completed by showing that $\Delta V(x) < 0$ for all $x > 0$ and $x \neq x^*$. This is done by considering separately four possibilities as depicted in Figure 4.

(1) Let $0 < x < x^*$ and $x < F(x) \leqq x^*$. We have

$$\begin{aligned}\Delta V(x) &= [R(F(x)) - F(x)] - [R(x) - x] \\ &= [R(F(x)) - R(x)] + [x - F(x)] \\ &> 0,\end{aligned}$$

because R is a monotonic decreasing function and $F(x) > x$.

(2) Let $0 < x < x^*$ and $x^* < F(x) < R(x)$. We have

$$\begin{aligned}\Delta V(x) &= [F(x) - S(F(x))] - [R(x) - x] \\ &= [F(x) - R(x)] + [x - S(F(x))].\end{aligned}$$

The function S is monotonic decreasing and by assumption $R(x) > F(x)$. It follows that $S(F(x)) > S(R(x)) = x$. Hence $\Delta V(x) < 0$.

(3) Let $x < x^*$ and $\max(0, S(x)) < F(x) \leqq x^*$. We have

$$\begin{aligned}\Delta V(x) &= [R(F(x)) - F(x)] - [x - S(x)] \\ &= [R(F(x)) - x] + [S(x) - F(x)].\end{aligned}$$

The function R is monotonic decreasing and $F(x) > S(x)$ by assumption. It follows that $R(F(x)) < R(S(x)) = x$. Hence $\Delta V(x) < 0$.

(4) Let $x > x^*$ and $x^* < F(x) < x$. We have

$$\begin{aligned}\Delta V(x) &= [F(x) - S(F(x))] - [x - S(x)] \\ &= [F(x) - x] + [S(x) - S(F(x))] \\ &< 0,\end{aligned}$$

because S is monotonic decreasing and $F(x) < x$.

So far we have restricted our attention to functions F which are continuous on $(0, \infty)$. If we have a function which is discontinuous at the equilibrium point, but continuous elsewhere, then clearly we can no longer have stability, either local or global. However, the equilibrium point may still be a global attractor, i.e. $x_n \to x^*$ as $n \to \infty$ for any initial $x_0 > 0$, and from a biological viewpoint this may be an acceptable property for some models (see Example 3(b)). The following two corollaries give sufficient conditions for the equilibrium point of (1) to be a global attractor. They essentially correspond to the cases $\theta=\pi/2$ and $\theta=0$ in the statement of Theorem 3.

COROLLARY 1. *Let F have a simple discontinuity from the left at x^* but be continuous elsewhere on* $(0, \infty)$ *and bounded on* $(0, x^*)$. *Then x^* of* (1) *is a global attractor if*

(a) $F(x)>x$ *for all* $x\in(0,x^*)$;
(b) $x^*<F(x)<x$ *for all* $x\in(x^*,\infty)$.

Proof. Since F is bounded for all $x\in(0,x^*)$ there exists $M>0$ such that $F(x)<M$ for all $x\in(0,x^*)$. Consider the function V defined by

$$V(x)=\begin{cases} M-x & \text{if } x\in(0,x^*),\\ x-x^* & \text{if } x\in[x^*,\infty). \end{cases}$$

V is not continuous at the equilibrium point but discontinuous "Liapunov-like" functions can be used to prove that an equilibrium point is an attractor (Kloeden and Fisher, 1978).

(1) Let $x>x^*$, we have

$$\begin{aligned}\Delta V(x)&=(F(x)-x^*)-(x-x^*)\\&=F(x)-x\\&<0.\end{aligned}$$

Hence for any initial $x_0\in(x^*,\infty)$, $x_n\to x^*$ as $n\to\infty$ since V is continuous on (x^*,∞) and $\Delta V(x)<0$.

(2) Let $0<x<x^*$. To prove $\Delta V(x)<0$ we need to consider two possibilities. Firstly, let $x<F(x)<x^*$. We have

$$\begin{aligned}\Delta V(x)&=(M-F(x))-(M-x)\\&=x-F(x)\\&<0.\end{aligned}$$

Secondly, let $x^*\leqq F(x)<M$. We have

$$\begin{aligned}\Delta V(x)&=(F(x)-x^*)-(M-x)\\&=(F(x)-M)+(x-x^*)\\&<0.\end{aligned}$$

Since F has a simple discontinuity from the left at x^*, $\lim_{x\to x^*_-} F(x) > x^*$ (we cannot have $\lim_{x\to x^*_-} F(x) < x^*$ since this would violate the condition $F(x) > x$ for all $x \in (0, x^*)$). Therefore there exists a $\delta > 0$ such that $F(x) > x^*$ for all $x \in (x^* - \delta, x^*)$ and then $x_n \to x^*$ as $n \to \infty$ for all $x_0 \in (x^* - \delta, x^*)$. Also, since $\Delta V(x) < 0$ for all $x \in (0, x^*)$, every trajectory initiating in $(0, x^*)$ must eventually enter $(x^* - \delta, x^*)$ or (x^*, ∞). Hence $x_n \to x^*$ as $n \to \infty$ for all $x_0 \in (0, x^*)$.

COROLLARY 2. *Let F have a simple discontinuity from the right at x^* and be continuous elsewhere on $(0, \infty)$. Then x^* of (1) is a global attractor if*

(a) $x < F(x) < x^*$ *for all* $x \in (0, x^*)$;
(b) $0 < F(x) < x$ *for all* $x \in (x^*, \infty)$.

Proof. Consider the V function defined by

$$V(x) = \begin{cases} x^* - x & \text{if } x \in (0, x^*]; \\ x & \text{if } x \in (x^*, \infty). \end{cases}$$

It can be shown that $\Delta V(x) < 0$ for all $x > 0$, $x \neq x^*$ and the proof follows by a similar argument to that used in Corollary 1.

Example 3. Let x_n be the number of fish in a year class in the nth generation and suppose that the number of fish in the next generation is given by the first equation in Table 1. If u_{n+1} is now defined as the number of fish harvested at time $n+1$, then

$$x_{n+1} = x_n[1 + r(1 - x_n/K)] - u_{n+1}. \tag{5}$$

The "maximum sustainable yield" (MSY) is given by $\bar{u} = rK/4$ and the corresponding MSY equilibrium is at $x^* = K/2$. We now consider two different harvesting strategies for model (5).

(a) Let

$$u_{n+1} = \begin{cases} 0 & \text{if } x_n \leqq 0.9x^*, \\ \bar{u}(10x_n/x^* - 9) & \text{if } 0.9x^* < x_n < x^*, \\ \bar{u} & \text{if } x_n \geqq x^*. \end{cases}$$

This corresponds to harvesting at MSY if the stock is above MSY level and reducing the catch by 10% for every 1% by which the stock falls short of the MSY level. This policy is similar to that used by the International Whaling Commission (I.W.C. Annual Report, 1976) for determining quotas

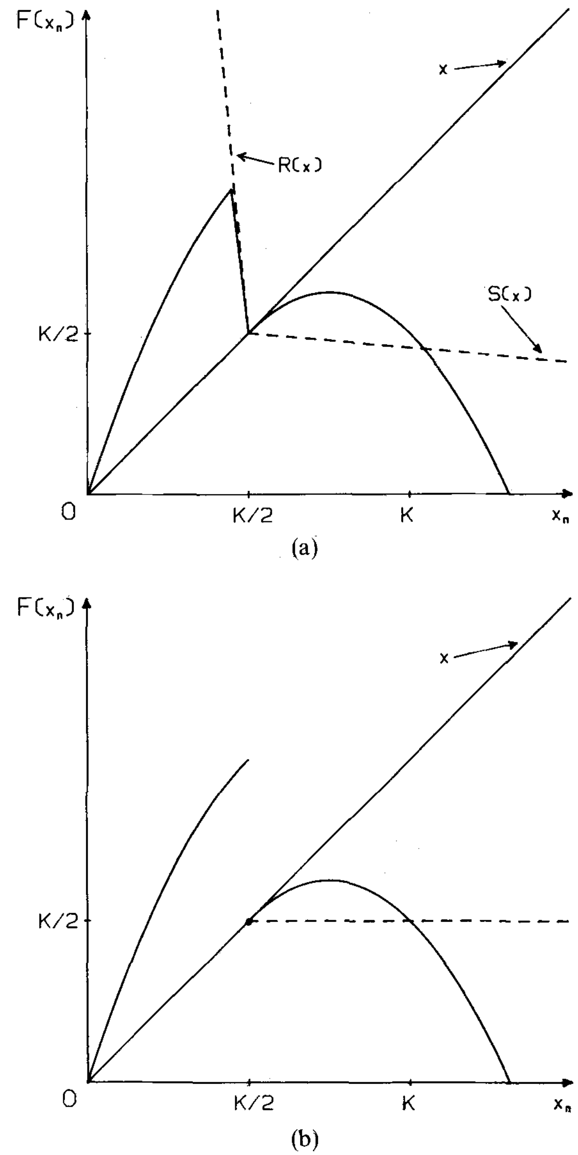

Figure 5. $F(x)$ as in equation (5) for the case $r=2$, with (a) u_{n+1} defined in Example 3(a); and (b) u_{n+1} defined in Example 3(b).

for some whale species. The graph of $F(x)$ corresponding to this definition of u_{n+1} is shown in Figure 5(a) for the case $r=2$.

If we choose $\tan^{-1} 9 \leqq \theta < \pi/2$ then we have that the equilibrium is stable by Theorem 3 (although not globally stable since the graph of $F(x)$ drops below that of $S(x)$ if x is large enough). Lines $R(x)$ and $S(x)$ corresponding to $\theta = \tan^{-1} 9$ are shown in Figure 5(a).

(b) An alternative harvesting strategy is given by

$$u_{n+1}=\begin{cases}0 & \text{if} \quad x_n<x^*,\\ \bar{u} & x_n \geqq x^*,\end{cases}$$

i.e. if the stock level falls below the MSY level stop harvesting otherwise harvest at MSY. $F(x)$ for this case is shown in Figure 5(b) with $r=2$. F In this example satisfies the conditions of Corollary 1 (provided we restrict x to a suitable neighbourhood of x^*) and so $x^*=K/2$ is a local attractor although x^* is not locally stable.

At this point it is worth commenting on the continuity requirements imposed on the function F in Theorem 3 and its two corollaries. For nearly all models, either biological or otherwise, F would be continuous except perhaps in the presence of a control as typified in example 3(b). In this case there would be a simple discontinuity at the equilibrium point and F would be continuous elsewhere. Theorem 3 and its two corollaries are still valid however if we allow f to have discontinuities at points other than the equilibrium point (the only exception being limit points of F on the line $F(x)=x$). For example, the model with

$$F(x)=\begin{cases}x^*+(x-x^*)/2 & \text{for} \quad x>0 \quad \text{and} \quad x \quad \text{irrational},\\ x^*+(x-x^*)/4 & \text{for} \quad x>0 \quad \text{and} \quad x \quad \text{rational},\end{cases}$$

is globally stable. The proofs of Theorem 3 and its corollaries can be modified to cover the more general case of F discontinuous but these proofs have been omitted here in an attempt to keep the presentation as simple as possible. For a proof of an analogue of Corollary 1, without the continuity restriction on F, the reader is referred to Kloeden and Fisher, 1978.

For completeness we include a final theorem on instability.

THEOREM 4. *The equilibrium point x^* of* (1) *is unstable if there exists $\theta \in (0, \pi/2)$ such that for some open interval I containing x^* we have*

(a) $F(x)>R(x)$ *or* $0<F(x)<x$ *for all* $x \in I, x<x^*$;
(b) $0<F(x)<S(x)$ *or* $F(x)>x$ *for all* $x \in I, x>x^*$.

Proof. As for Theorem 3 we define

$$V(x)=\begin{cases}R(x)-x & \text{if} \quad x \in (0, x^*],\\ x-S(x) & \text{if} \quad x \in (x^*, \infty).\end{cases}$$

$V(x)>0$ for all $x>0$, $x\neq x^*$. It can be shown that $\Delta V(x)>0$ for all $x\in I, x\neq x^*$ in a manner similar to that used in the proof of Theorem 3. Hence we have that x^* of (1) is unstable.

APPENDIX

From Example 2 we have

$$\Delta V(x)=(x\exp[r(1-x/K)]-K)^2-(x-K)^2$$
$$=xh(x)(\exp[r(1-x/K)]-1),$$

where

$$h(x)=x\exp[r(1-x/K)]+x-2K.$$

To prove that $\Delta V(x)<0$ for all $x>0, x\neq x^*$ and $0<r<2$ it is sufficient to prove that $h(x)<0$ for $x\in(0,K)$ and $h(x)>0$ for $x\in(K,\infty)$. The proof is by contradiction.

Suppose that $h(x)>0$ for some $x\in(0,K)$. Since $h(0)<0$, $h'(K)>0$ for $0<r<2$ and $h(K)=0$, h'' must have at least one zero in $(0,K)$. But

$$h''(x)=-(r/K)\exp[r(1-x/K)](2-rx/K)<0$$

for $0<r<2$ and $x\in(0,K)$. Hence $h(x)<0$ for all $x\in(0,K)$ and $0<r<2$.

Now suppose that $h(x)<0$ for some $x\in(K,\infty)$. Then h must have a minimum at some point $y>K$ where $h(y)<0$ since $h'(K)>0$ for $0<r<2$ and $h(x)\to+\infty$ as $x\to+\infty$. y satisfies

$$\exp[r(1-y/K)]=\frac{1}{ry/K-1}>0,$$

and then

$$h(y)=\frac{y}{ry/K-1}+y-2K$$
$$=\frac{(r/K)(y-K)^2+K(2-r)}{ry/K-1}>0.$$

This is a contradiction. Hence $h(x)>0$ for all $x>K$, $0<r<2$.

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