DISCONTINUOUS SUSTAINABLE YIELD: THE EXCEPTION OR THE RULE?

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ABSTRACT

The sustainable yield function is a favoured tool in fisheries policy making. Normally, this function is drawn as a continuous curve in effort-yield space. This means that sustainable yield (harvest) is gradually reduced to zero as fishing effort increases. This, however, does not have to be the case. The sustainable yield function may easily be discontinuous in the sense that sustained fishing effort beyond a certain critical level will lead to a discrete fall in yield to zero, i.e., a collapse of the fishery. The corresponding sustainable yield curve then has a gap at the critical fishing effort level. Clearly, the existence of such a gap has major implications for fisheries policy.

It has long been recognized that depensatory biomass growth generally leads to discontinuous sustainable yield curves. What appears to be less well understood is that with fully compensatory biomass growth, fish schooling (patchy distribution of fish over the fishing grounds) generally leads to the same result. Since schooling behaviour is typical of most species of fish — only the degree of schooling varies — discontinuous sustainable yield functions tend to be the rule rather than the exception.

This paper considers with these issues. It shows how schooling behaviour leads to discontinuities in the sustainable yield function. It explores the corresponding dynamics of the fish stock and the implications for the risk of stock collapses and fisheries policies designed to avoid them. The paper finally speculates about the impacts of profit maximizing investments by fishing firms on the existence and location of gaps in sustainable yield curves.

Keywords: Sustainable yield, sustainable biomass, discontinuous sustainable yield catastrophes,

INTRODUCTION

The sustainable yield function is a favoured tool in fisheries policy making. Normally, this function is drawn as a continuous curve in effort-yield space. This means that as fishing effort is increased beyond a certain level (the maximum sustainable yield level) sustainable yield (harvest) is gradually reduced to zero. This, however, does not have to be the case. The sustainable yield function may easily be discontinuous in the sense that sustained fishing effort beyond a certain critical level will lead to a discrete fall in yield to zero, i.e., a collapse of the fishery. Clearly, the existence of such a discontinuity has major implications for fisheries policy.

It has long been recognized (see e.g. [1]) that depensatory biomass growth may lead to what amounts to discontinuity in the sustainable yield curve. What appears to have been overlooked in the literature is that common features of the harvesting process can easily generate the same result, even when the biomass growth function is fully compensatory. One such feature is the impact of fish schooling (patchy distribution of fish over the fishing grounds) on the harvesting function. Since a degree of

schooling behaviour is typical of many species of fish, discontinuous sustainable yield functions may be the rule rather than the exception.

This paper explores this issue. It begins by illustrating on the basis of a standard aggregative fisheries model, how discontinuities in sustainable yield and biomass curves may arise. It then goes on to analyze the model structure responsible for these discontinuities. It is shown that discontinuities in sustainable yield and biomass are manifestations of a well-known mathematical catastrophe called the fold catastrophe. This catastrophe is likely to arise if the net biomass growth function, i.e., the natural biomass growth less harvest, is not strictly concave. That the net biomass growth function is non-concave seems empirically to be the rule rather than the exception. Among the implications of the fold catastrophe is that more that the same fishing effort maps into more than one sustainable yield and biomass. Consequently, strictly speaking, a sustainable yield function does not really defined. The paper concludes by some observations on the dynamics corresponding to discontinuous sustainable yield functions.

SETTING THE STAGE

A general aggregative fisheries model may be written as (see e.g. [2]):

$$\dot{x} = G(x) - y , \ x, y \geq 0 , \tag{1}$$

$$y = Y(e, x), \ x, y, e \geq 0 \tag{2}$$

In this formulation, x represents fish stock biomass and $\dot{x}$ the first derivative of biomass with respect to time. y the volume of harvest and e fishing effort. The function $G(x)$ is the natural biomass growth function and the function $Y(e,x)$ is the harvesting function. The functions $G(x)$ and $Y(e,x)$ are assumed to be twice continuously differentiable (which implies both functions are continuous over their allowed domain). The function $G(x)$ is assumed to pass through the origin, and have the property that $G(x){>}0$ for $\overline{x} > x > 0$ and $G(x){<}0$, for $x > \overline{x}$. Note that $G(x)$ does not have to be concave. So, it allows depensation [3,1]. The function $Y(e,x)$ is assumed to be monotonically increasing in both its arguments, jointly concave and $Y(e,0){=}Y(0,x){=}0$.

In biomass equilibrium, $\dot{x} = 0$. This implies that the function:

$$\Gamma(e, x) \equiv G(x) - Y(e, x) = 0 . \tag{3}$$

The function $\Gamma(e, x)$ will play an important role in what follows.

If biomass equilibrium exists, (1) and (2) define implicit mappings from fishing effort to sustainable harvests and biomass.

$$\Psi : e \rightarrow y \tag{4}$$

$$\Theta : e \rightarrow x \tag{5}$$

Under certain, as it turns out quite restrictive, conditions these mappings define functions. In that case, the former is referred to as the sustainable yield function [1]. Corresponding to this terminology the latter may be referred to as the sustainable biomass function.

At this stage it is useful to note that if a sustainable biomass function is not defined, a sustainable yield function is not defined either. To see this it is sufficient to observe that according to (2), harvests depend on biomass. The same observation shows that if the sustainable biomass function exists and is

discontinuous, the sustainable yield function must be discontinuous at the same level of fishing effort. It follows that to study discontinuities in the sustainable yield function it is sufficient to study the sustainable biomass function.

It is well established by e.g. [1] that in the case of biomass growth depensation, the mapping in (4) does not define a unique function. So, in that case, it is strictly speaking not accurate to talk about a sustainable yield function at all. Moreover, at a certain critical effort level, e^*, say, the relationship between fishing effort and harvest undergoes a bifurcation as Clark [1] refers to it and is qualitatively altered. The slope of the sustainable yield and biomass functions becomes infinite. The functions become what amounts to discontinuous and alternative unstable yield and biomass functions emerge.

It is possible to establish the essence of the above assertion in a simple graphical way. A depensatory biomass growth function is drawn in Figure 1 as a function of biomass. Also in the same figure three harvesting functions for different levels of fishing effort are drawn. The vertical axis in the diagram measures biomass growth and harvest (which are measured in the same units). From the diagram it is evident that over a certain range of fishing effort, more precisely e_0 to e^*, fishing effort maps into two different sustainable harvest and biomass levels. In other words, these mappings from fishing effort to sustainable yield and biomass cannot be represented as a
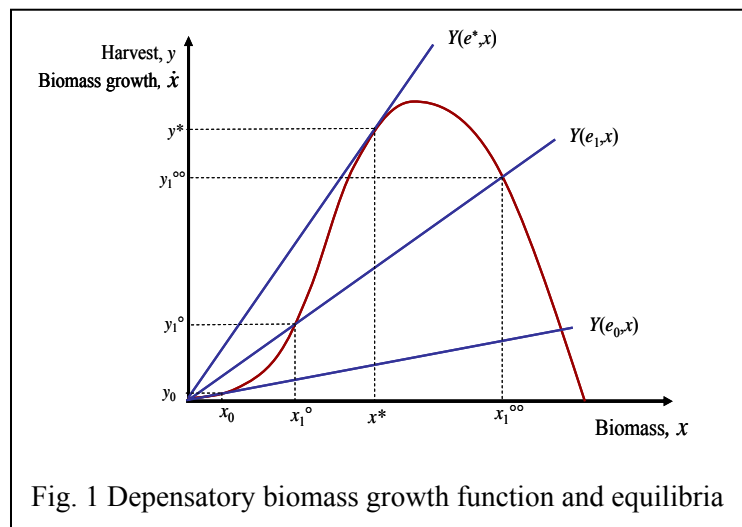

Fig. 1 Depensatory biomass growth function and equilibria

unique function. In fact, in this particular case, the mapping defines two sustainable functions for both harvest and biomass, one of which is unstable. These functions are illustrated in Figure 2. The solid curves correspond to stable sustainable segment of the sustainable relationship and the dashed curves to the unstable part. At fishing effort level e^* in Figures 1 and 2 a bifurcation occurs. The relationship between fishing effort and sustainable yield and biomass qualitatively changes. An infinitesimal increase in fishing effort beyond e^* will lead to no sustainable yield or biomass. In this sense there is a discontinuity in the sustainable curves.
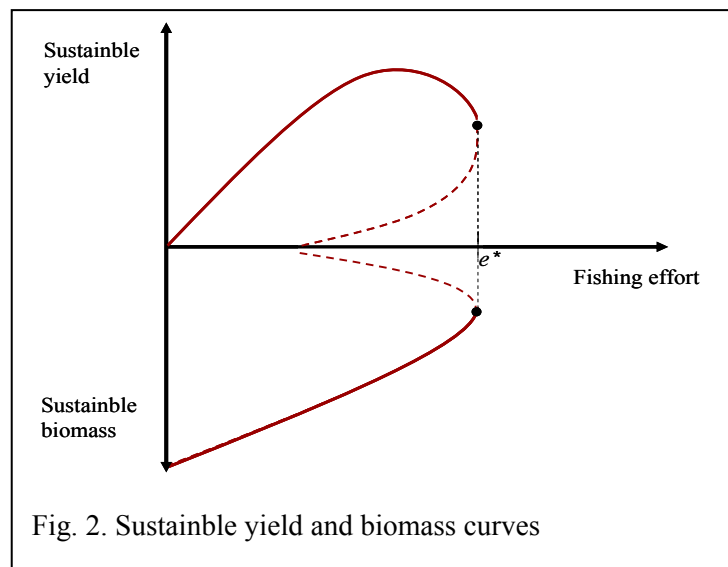
The bifurcation illustrated at e^* in Figure 1 corresponds to a special type of a mathematical catastrophe called the fold catastrophe [4]. This as other elementary catastrophes occurs when a function and

Fig. 2. Sustainble yield and biomass curves

its derivative are simultaneously zero. In this particular case, $\Gamma(e^*, x) = 0$ because of equilibrium. Moreover, at the same point $\Gamma_x(e^*, x) \equiv G_x(x) - Y_x(e^*, x) = 0$ as can be verified from Figure 1.

The situation illustrated in Figure 2 should be compared with the conventionally analyzed case where the biomass growth function is strictly concave (compensatory). In that case, it is easy to check that the mappings in (3) and (4) define unique functions, which are continuous and without any points of collapse (catastrophe, bifurcation).

All of this was established decades ago by [1]. What does not seem to have been realized is that this discontinuity does not at all depend on a depensatory biomass growth function. In fact, a depensatory biomass growth function is neither necessary nor sufficient for the catastrophe to occur and the sustainable curves to be discontinuous. A necessary and sufficient condition for this is merely that the function $\Gamma(e, x)$, defined in (3) above, be nonconcave in x over some relevant range of biomass. Since $\Gamma(e, x)$ is the difference between the biomass growth function and the harvesting function, this can obviously happen even if both functions are concave in biomass.

As an example consider the case where both $G(x)$ and $Y(e,x)$ are strictly concave in biomass. A strictly concave $G(x)$ is of course the usual biomass growth function considered in fisheries economics. A harvesting function strictly concave in x could for instance reflect less than perfect dispersion of fish on the fishing grounds (a degree of schooling behaviour by the fish), so that harvest does not increase proportionately with fishing effort [5,6]. The effect of this can be illustrated in a way similar to the above. In Figure 3 a perfectly concave biomass growth function is drawn. Similarly a couple of strictly concave harvesting function for two different levels of fishing effort are drawn. It is readily seen that fishing effort such as e_1, maps into two levels of sustainable harvest and biomass. So, for this level of fishing effort there are two sustainable curves. Fishing effort e^*, however, maps into only one sustainable harvest and biomass level. So at e^* the two sustainable curves cease to exist. e^* is a point of catastrophe. An infinitesimal increase in fishing effort beyond e^* generates no sustainable biomass or harvest.
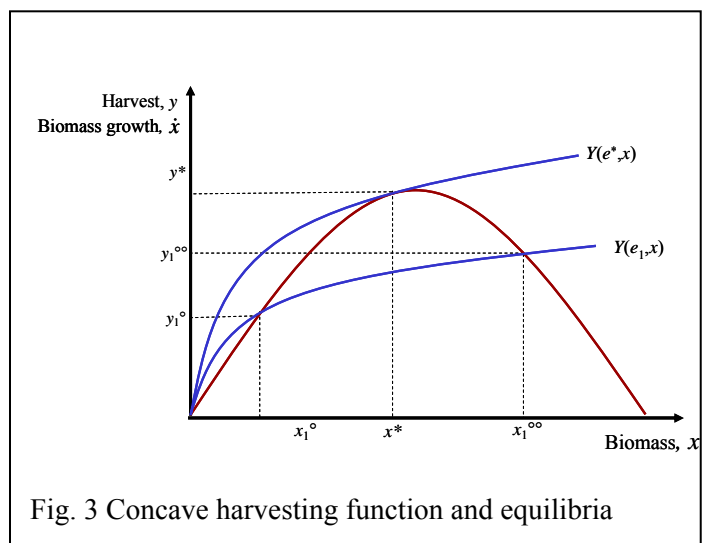
A computer generated example of

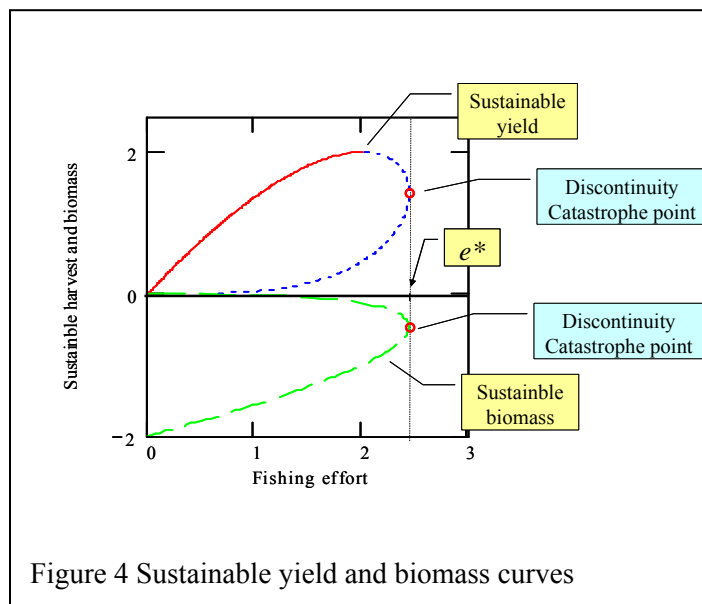Fig. 3 Concave harvesting function and equilibria

Figure 4 Sustainable yield and biomass curves

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sustainable yield and biomass curves corresponding to Figure 3 is presented in Figure 4. The fold catastrophe occurs at e^* which is also a point of discontinuity. Note the similarities between this figure and the diagram in Figure 2 above. This suggests that as far as discontinuities in the sustainable functions are concerned, there is no essential difference between the effects of depensatory (especially critically depensatory [1] biomass growth functions and a harvesting function concave in biomass.

ANALYSIS

As discussed in section 1, net biomass growth may be written as the function:

$$\Gamma(x,e) \equiv \dot{x} = G(x) - Y(e,x).$$

The function $\Gamma(x,e)$ is extremely helpful in the analysis of discontinuities (catastrophes, bifurcations) in sustainable biomass and yield curves. In that context, the relevant biomass interval over which to study $\Gamma(x,e)$ is $[0,\overline{x}]$, where $\overline{x}$ is the biomass carrying capacity.

The function $\Gamma(x,e)$ has some useful properties most of which are quite obvious.

(i) $\Gamma(x,e)$ is continuous and is twice continuously differentiable for all $x \in (0,\overline{x})$.

   This follows immediately from the assumption that its constituent functions $G(.)$ and $Y(.,.)$ have this property.

(ii) $\Gamma(0,e) = 0$.

(iii) $\Gamma(\overline{x},e) \leq 0$, for all $e{\geq}0$, $\Gamma(\overline{x},0) = 0$ and $\Gamma(\overline{x},e) < 0$, $e{>}0$.

(iv)   For biomass equilibrium, $\Gamma(x,e) = 0$.

(v)   Provided $x{>}0$, $\Gamma(x,e)$ is falling in e.

   This follows immediately from $\Gamma_e(x,e) = -Y_e(e,x)$.

(vi) $\Gamma(x,e_1) \neq \Gamma(x,e_2)$, $e_1 \neq e_2$ unless $x{=}0$. In other words, Γ-curves can not cross except at the origin.

   This follows immediately from the assumption that $Y_e(e,x) > 0$

(vii) $\Gamma(x,e)$ is not necessarily concave in x, even if both $G(.)$ and $Y(.,.)$ are.

   Difference of two concave functions is not necessarily concave.

From the perspective of this study, property (vii) is crucial. If $\Gamma(x,e)$ is not concave, the sustainable relationships may be subject to fold catastrophes which imply (a certain type of) discontinuities and other irregularities with potentially deep-reaching practical implications.

Let us first consider the case of a strictly concave Γ-function. Figure 5 depicts three such Γ-curves for different levels of fishing effort. By the above properties of the Γ-function (properties (i)-(iii)) all such curves are continuous, smooth, must begin at the origin and end at $\overline{x}$ with a non-positive $\Gamma(x,e)$. The first (uppermost) curve is drawn for fishing effort equal to zero. This replicates the natural biomass growth function. The other two curves are drawn for positive levels of fishing effort.

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Biomass equilibrium requires $\Gamma(x,e) = 0$. Thus points where $\Gamma(x,e)$ intersects the horizontal axis are biomass equilibrium points. There are two such equilibria for each level of fishing effort, one at the origin (x=0) and one for a positive level of biomass. Note that as fishing effort increases, the non-zero biomass equilibria converges to the origin (Γ-curves fall with fishing effort; property (v)). For a sufficiently high fishing effort, the $\Gamma(x,e)$-curve would never enter the positive quadrant and there would be no non-zero biomass equilibrium. These observations demonstrate that for a

Fig. 5 Possible Γ-curves: the concave case

concave Γ-function, a sustainable biomass function exists and is continuous and monotonically falling in fishing effort.
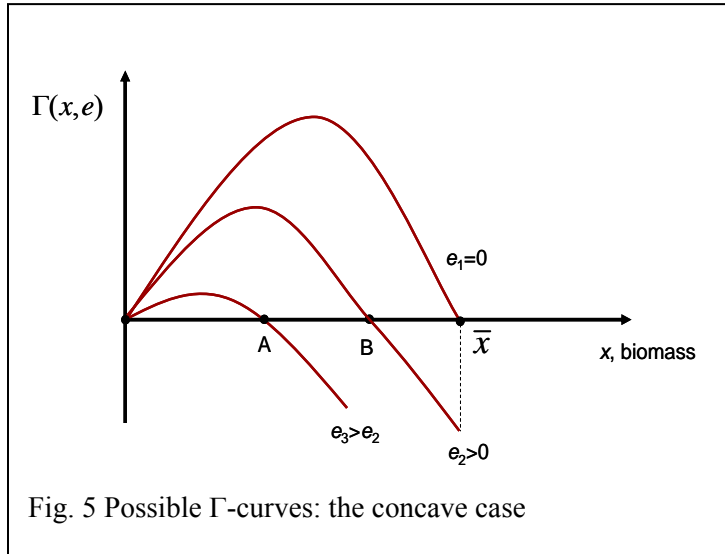
Note that the existence of a continuous sustainable biomass curves implies the existence of a similarly continuous sustainable yield curve. This is because by (2) sustainable yield is simply:

$$y = Y(e, \Theta(e)),$$

where $\Theta(e)$ is the sustainable biomass function and the function $Y(.,.)$ is continuous by assumption.

Note further that the positive equilibrium points depicted in Figure 5 are all locally stable. This is because at these points the slope of $\Gamma(x,e)$ is negative, i.e. $\partial \dot{x}/\partial x < 0$. The equilibrium at the origin (x=0), by contrast, is unstable, provided a stable equilibrium exists for some fishing effort. This proves that in the case depicted in Figure 5, the sustainable biomass and yield curves are stable in the sense that if fishing effort is kept constant, biomass and yield will converge to the corresponding point on the curves. This stability, of course, is what is usually implicitly assumed when these curves are presented.

Now, according to property (vi) there is no reason for $\Gamma(x,e)$ to be concave in x for all levels of fishing effort, e, compatible with equilibrium. One possible example of the case of non-concave Γ-function is illustrated in Figure 6.

As illustrated in Figure 6, if there is no fishing effort, the Γ-function simply traces out the biomass growth function (assumed to be concave). However, for some positive levels of fishing effort, the Γ-function may have be the shape illustrated in Figure 6. In that case, there are two positive biomass equilibrium points for some range of fishing
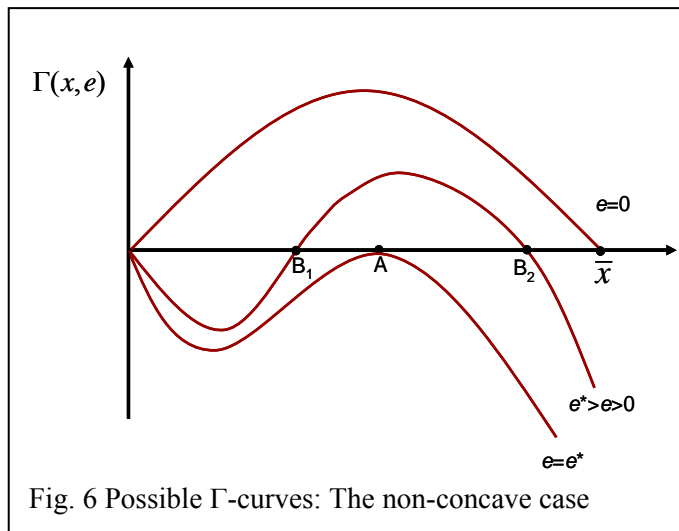

Fig. 6 Possible Γ-curves: The non-concave case

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effort. Examples of these are B_1 and B_2 in Figure 6. B_1 is an unstable biomass equilibrium ($\Gamma_x(B_1,e) > 0$) and B_2 a locally stable one ($\Gamma_x(B_2,e) < 0$) [7].

If two equilibrium points exist, there must also exist a level of fishing effort such that a biomass point like A exists. The reason is that $\Gamma(x,e)$ is continuous and falling in e for every positive x (property (v) above). Moreover, for all positive levels of biomass, $\Gamma(\overline{x},e) < 0$ (property (iii)). Finally, outside the origin Γ-curves can never cross (property (vi)). Thus, obviously a point like A must exist.

In the formal language of catastrophe theory, point A corresponds to a fold catastrophe [5]. Such a catastrophe occurs if at some point (x^*,e^*), say, $\Gamma(x^*,e^*) = 0$, i.e. equilibrium prevails and

$$\Gamma_x(x^*,e^*) = 0 .$$

Clearly, these conditions are satisfied at point A in Figure 6. At points of catastrophe, the system in question exhibits a drastic change in qualitative behaviour. This is exactly what happens to the sustainable curves at fishing effort level e^*. First a tiny increase in fishing effort leads to a discontinuous jump in sustainable biomass and harvest to zero. Second, the sustainable curves spit into two alternatives; (a) the previous stable sustainable functions and (b) unstable but sustainable biomass and yield functions (the lower branches in Figures 2 and 4). Third the second of these functions, the unstable ones are quantitively different from their stable counterparts and qualitatively different (in being unstable). At the lower branch a slight increase in fishing effort leads to collapses to zero. A slight decrease in fishing effort leads to a shift to the stable branch.

Besides representing a mathematical catastrophe, point A corresponds to a discontinuity in the sustainable biomass curve as well as the sustainable yield curve. At fishing effort level e^* both of these curves exhibit infinite slopes as illustrated in Figures 2 and 4 in section 1. To see this, note that in equilibrium, the basic fisheries model defined by (1) and (2) implies the following (comparative statics) derivatives:

$$\frac{dx}{de} = \frac{Y_x}{\Gamma_x} ,$$

$$\frac{dy}{de} = \frac{Y_e \cdot G_x}{\Gamma_x} .$$

Obviously, if $\Gamma_x \to 0$, these derivatives (slopes) approach $\pm \infty$ which is a defining feature of fold catastrophes as illustrated in Figures 2 and 4 above.

The above suggests that the curvature (concavity/non-concavity) properties of the Γ-function are crucial for the existence of catastrophes and consequently discontinuities in the sustainable functions. In particular, if the Γ-function is strictly concave, there can be no discontinuities in sustainable curves.

Theorem 1
A necessary condition for a discontinuity in sustainable curves

A necessary condition for an unstable equilibrium is that $\Gamma_{xx}(x,e) > 0$ over some $x-$ segment $\in [0,\overline{x}]$.

Proof: Let the unstable equilibrium be at biomass x'. Thus $\Gamma(x',e)=0$. Unstable equilibrium requires $\Gamma_x(x',e)>0$. So for the unstable equilibrium to exist, Γ must have hit the x-axis from below. But $\Gamma(0,e)=0$. Therefore to reach $\Gamma(x',e)=0$, $\Gamma_{xx}(x,e)>0$ over some interval.

Theorem 1 conveys two important messages. First, if the Γ-function is concave the sustainable function are guaranteed to be continuous. If the Γ-function is not concave, the sustainable functions may exhibit discontinuities and catastrophes.

Simple sufficient conditions for discontinuities in the sustainable functions do not seem to be easy to come by. The following theorem may offer some help.

Theorem 2
A sufficient condition for a discontinuity in sustainable curves

A sufficient condition for an unstable equilibrium to exist is that $\Gamma_x(0,e)<0$ for some e which is compatible with a non-zero equilibrium.

Proof: If $\Gamma_x(0,e)<0$, it follows that $\Gamma(\varepsilon,e)>0$ for sufficiently small $\varepsilon>0$. Therefore, since a non-zero equilibrium has been assumed to exist and $\Gamma(x,e)$ is continuous, an unstable equilibrium must exist.

So, if $\Gamma_x(0,e)<0$ at zero biomass and a sustainable equilibrium exists, there will be a discontinuity in equilibrium curves. An example is the schooling fishery:

$$\Gamma(x,e) \equiv \dot{x} = \alpha \cdot x - \beta \cdot x^2 - q \cdot e \cdot x^\delta, \text{ where } \delta<1.$$

This suggests that all schooling fisheries (i.e. fisheries whose harvesting functions can be expressed as $y = \phi(e) \cdot x^\delta$ where $\delta<1$) and biomass growth functions with finite intrinsic growth rate will exhibit discontinuous sustainable functions.

The following further results are fairly obvious and stated without proof:

Assertion 1: If there is an unstable equilibrium (over some finite interval of e) then there is a stable equilibrium as well.

Assertion 2: A discontinuity in one sustainable function implies a discontinuity in the other (at the same level of fishing effort)

Assertion 3: A discontinuity in a sustainable function implies a mathematical catastrophe at the same point and vice versa.

Assertion 4: If the Γ-function is non-concave there can be multiple equilibrium curves.

The last assertion has considerable practical implications. The existence of multiple equilibrium curves suggests more than one stable sustainable yield curve one at a higher yield level than the other. Thus, a fishery may get stuck in an inferior sustainable yield region from which it might be difficult to escape.

SOME ELEMENTARY DYNAMICS

In a series of papers in the 1940s, Samuelson [8,9] explained the relationship between comparative statics, stability and dynamics which he referred to as the Correspondence Principle. The Correspondence Principle applies to the subjects of this study. The sustainable relationships are equilibrium relationships brought about by dynamic forces. Catastrophes occur at points where these dynamics are radically altered and the equilibrium relationships shift or cease to hold altogether. In this section, the dynamics corresponding to the sustainable relationships will be briefly touched upon. These dynamics are extremely important because they explain the evolution of the fishery outside the sustainable curves and, in particular, highlight the traps which await fisheries managers at the discontinuities in the sustainable curves. These are complicated subjects and what is presented here should rather be regarded as examples rather than an attempt at a coherent analysis.

First let's consider the case where there are only two non-zero equilibria. For simplicity and transparency, we restrict our attention to the dynamics of harvest. In that case, we may illustrate the most relevant dynamics in yield-effort space as in Figure 7. The curves drawn are the sustainable equilibrium curves. The solid one is the stable

Fig. 7 Dynamics in Yield effort space

branch of the equilibrium relationship. The dashed curve is the unstable branch. The arrows indicate the motion of harvest for <u>fixed</u> fishing effort. Note that given fixed effort, there is a one-to-one, positive relationship between the movement in harvest and the movement in biomass. Thus, when harvest is increasing, biomass must also be increasing and vice versa.
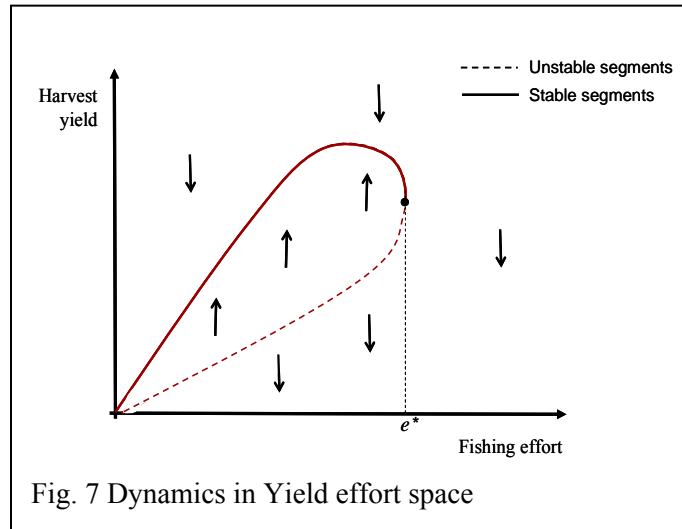
It is worth noting that the dynamics split the harvest-effort space into two regions. The region of stability is above the unstable segment of the sustainable harvest curve up to e^*. The rest of the positive quadrant is a region of instability.

As illustrated in the diagram, initially as fishing effort increases, harvest tends to converge to stable sustainable levels. At a certain level of fishing effort, not greatly in excess of the maximum sustainable yield, a point of catastrophe is met expressed as a discontinuity in the stable segment of the sustainable yield. Any fishing effort level beyond e^* is in the region of instability and leads to a sustained drop in harvest (and biomass) toward zero.

For practical fishery management, the first advice is to maintain fishing effort well below the catastrophe point, e^*. Since the location of that point is generally not well known, the sound policy is never to exceed the fishing effort corresponding to maximum sustainable yield. The second advice concerns what do to do if the fishery is suspected to have entered the unstable region. If that happens, the safest course is to cut back on fishing effort quite drastically. Anything less than a drastic cut back runs the risk of remaining in the unstable region with biomass and harvest still declining. Obviously, from Figure 7, the longer the fishery has remained in the unstable region, the greater will the effort reduction

necessary to restore the fishery have to be. A failure to reduce fishing effort drastically enough may have contributed to the demise of certain important ocean fisheries (e.g. the Northern cod fishery).

Let us now consider the possibility that there are three non-zero equilibria. Then we might see a sustainable yield function as in Figure 8. Notice that in this case, for certain levels of fishing effort, there are in fact three sustainable curves. The middle one is unstable, as shown in the diagram. The other two are stable. Note in particular that there are two stable sustainable functions for high levels of fishing effort. One of them yields comparatively high harvests. This is the one which is usually taken for granted in fisheries economic analysis. The other one produces much less harvest. However, since it is stable, it might be difficult to get out of its region of attraction. Quite possibly, the existence of such low yield stable sustainable segments may explain the experience in some depressed fisheries.
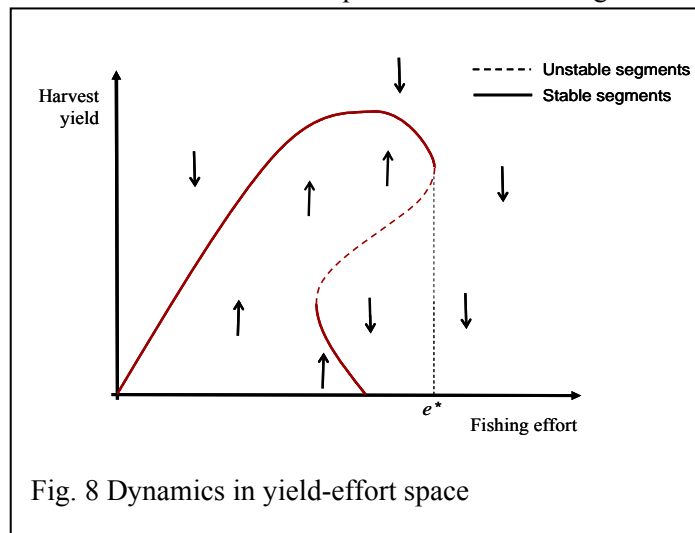

Fig. 8 Dynamics in yield-effort space

Although the dynamics depicted in Figure 8 are more complicated than those in Figure 7, the practical management advice is largely the same. First, be careful to avoid the point of discontinuity. Second, if the fishery is suspected to have left the uppermost stable sustainable, radically reduce fishing effort in an attempt to bring the fishery into its field of stability. Third, be careful not to get stuck at the lower branch of stable sustainable yield.

DISCUSSION

Catastrophe points in the $\Gamma(e,x)$-function correspond to a discontinuity in the stable part of the sustainable yield and biomass functions. These discontinuities have substantial practical implications. Basically these implications are adverse. For a fishery which has been travelling approximately sustainably along an effort-expanding path, hitting the discontinuity means that sustainability suddenly disappears and the fishery experiences a persistent decline in harvest and biomass. Many fisheries may be in danger of experiencing this and some probably already have. For fisheries which have already suffered the catastrophe, i.e. exceeded the point of discontinuity, the travel back to the stable sustainable yield curve requires a reduction, often quite a substantial one, in fishing effort. Thus the catastrophe cannot be exploited in the other direction. For the fishery it is truly a one-directional catastrophe.

Catastrophe points in the $\Gamma(x,e)$ function may and are in fact likely to occur if the $\Gamma(x,e)$ function is not strictly concave in biomass. The $\Gamma(x,e)$ function is the difference between the natural biomass growth function and the harvesting function. This function may be non-concave if (i) the biomass growth function is not concave (e.g. exhibits a level of depensation) or (ii) if the harvesting function is concave in biomass. The first case, depensation in biomass natural growth function is well established for many species. Regarding the harvesting function; there are ample reasons to expect it to be strictly concave in biomass. One of them is less than perfect dispersion of fish on the fishing grounds (i.e. a degree of fish schooling). This feature is undoubtedly very common among fish stocks. For that reason already,

harvesting function may be expected to be concave in biomass. Another reason for concavity are upper bounds on harvest which may occur e.g. because of capacity constraints or even man made constraints on harvesting capacity.

Since, non-concave $\Gamma(e,x)$ function are for empirical reasons highly likely, it follows that discontinuities in sustainable yield and biomass functions are too. In fact, it seems that they may well be rule rather than the exception. If so, fisheries management, especially at relatively low levels of biomass, may be substantially more complicated than has been appreciated in the past.

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