



An Augmented Clark Model for Stability of Populations

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ABSTRACT

A simple modification of a frequently employed age-structured model for population dynamics is presented. This augmented formulation allows the assessment of the impact of age-dependent harvest mortality on population stability. The characteristic frequencies of the predicted oscillations are discussed. The period of oscillation is almost independent of survival and the exact functional form of the recruitment function, and it is not equal to twice the mean age of mature animals, as suggested earlier. It is shown that increased survival before reproduction has a destabilizing influence for populations exhibiting an overcompensatory recruitment function.

1. INTRODUCTION

Population dynamics models provide an essential tool for the design of animal harvest management strategies. Modeling efforts seek optimal equilibrium harvests, but in addition to this goal these studies must consider the effect of yield targets on population stability (e.g., [1, 2]). Care must be exercised to avoid the exacerbation of natural fluctuations by management policy changes, in order that stock collapses not be precipitated. The dynamics of populations with overlapping generations have been greatly simplified by the Clark [1] model (so termed by Botsford [3]), which circumvents the need for a matrix formulation. The Clark model was applied by Goh and Agnew [2] to investigate the effect of changing fishing mortality on stock stability.

An important parameter in harvest theory is the spawning biomass produced per recruit, which, with the mortality rate, controls the slope of the replacement line and thus determines the equilibrium population. (A *recruit* is a fish reaching a specified age in a given year; *recruitment* is the number of recruits appearing in the given year.) Although recruitment-based population models are most widely applied to fish populations, they have also been extensively applied to mammal and insect populations [4]. In the general context, the yield of spawners

per recruit would be the yield of adults per pup, cub, kitten, etc. In the brief study to follow we show how the number of spawners produced per recruit influences the stability of a population. This requires a slight modification of the Clark model. The formulation presented allows an appraisal of the effect of age-dependent (differing between juveniles and adults) harvest mortality on population stability.

2. MODEL FORMULATION AND APPLICATION

In this section we derive a simple variant of the Clark model that allows incorporation of the spawners-per-recruit parameter. By linearizing the dynamical equation, a characteristic equation for population stability is obtained. A previously somewhat neglected aspect, the period of the population oscillations, is discussed in some detail. We complete this section with a treatment of population stability as a function of the spawners-per-recruit parameter and draw conclusions about the implications of the result for harvest policy.

We commence with the following relation for the number of spawners in year n (S_n):

$$S_n = lS_{n-1} + (l_p)^k Z_{n-k}, \quad (1)$$

where l is the annual survival fraction for spawners, l_p is the annual survival fraction for prespawners, k is the age of maturity (all animals are assumed to mature at age k), and Z_{n-k} is the number of animals born in year $n-k$. If recruitment is deemed to occur at age j , then the year class strength resulting from spawning in the year $n-k$ is simply $Y_{n-k} = (l_p)^j Z_{n-k}$ and (1) becomes

$$S_n = lS_{n-1} + (l_p)^{k-j} Y_{n-k}. \quad (2)$$

We recognize that $(l_p)^{k-j}$ is simply the number of spawners per recruit (designated σ here), and with the notation $Y_{n-k} \equiv F(S_{n-k})$ we have the following equation for the population dynamics:

$$S_n = lS_{n-1} + \sigma F(S_{n-k}). \quad (3)$$

According to Equation (3), the equilibrium number of spawners (S_0) and recruitment (F_0) are related by the familiar form

$$F_0 = \frac{1-l}{\sigma} S_0. \quad (4)$$

Since $(1-l)S_0$ spawners perish each year, it follows that $(1-l)S_0/\sigma$ recruits are required to replace them. Thus, the so-called replacement line (Figure 1) is simply a line through the origin of the $S_n, F(S_n)$ plane with a slope of $(1-l)/\sigma$. The replacement line concept provides a convenient picture of equilibrium: Equilibrium is the intersection of the replacement line with the stock–recruitment curve $F(S_n)$.

Figure 1 illustrates the variation of the replacement line and the equilibrium as σ changes. Increasing σ , corresponding to reduced mortality of juveniles, decreases the slope of the replacement line, causing changes in the slope of the stock–recruitment curve at equilibrium, a factor important to stability (see Section 2.1). Reduced mortality of juveniles could stem from reductions of the harvesting of these younger fish. Similarly, reduced fishing of spawners would increase l , again diminishing the slope of the replacement line. Thus, there is a clear link between harvest rates and stability. Figure 2 strikingly illustrates the possible effects of fishing on stability. The dashed line shows the replacement line for zero fishing mortality (natural mortality alone). The equilibrium for zero fishing mortality is apparently well to the right of the observed stock–recruitment trajectories, emphasizing the effect of fishing mortality in determining the equilibrium and, of course, the slope of the stock–recruitment function at equilibrium.

Figure 2 also depicts real examples of the domed recruitment functions illustrated in Figure 1. These domed curves are formally referred to as overcompensatory recruitment functions [those for which $dF(S_n)/dS_n$ becomes negative at sufficiently large S_n]. Only overcompensatory recruitment functions allow the existence of endogenous oscillations. Overcompensation is likely in cannibalistic fish species [5] such as saithe (*Pollachius virens*), also known as pollock in North America. (The curves shown in Figure 2 are derived from three saithe stocks.) Myers et al. [6] found evidence for overcompensation in 25% of the 300 or so fish stocks entered in their compilation.

Equation (3) is identical to the Clark model aside from the fact that Clark's model essentially fixes σ at a value of 1. Since we are interested in the influence of a varying σ on stability properties it is important that this quantity be retained in our analysis. Explicit dependence on σ could be eliminated by writing $\sigma F(S_{n-k}) = \tilde{F}(S_{n-k})$ so that

$$S_n = lS_{n-1} + \tilde{F}(S_{n-k}), \quad \tilde{F}_0 = (1-l)S_0.$$

However, this measure merely hides the σ dependence, which inconveniently becomes incorporated in the parameters of the recruitment

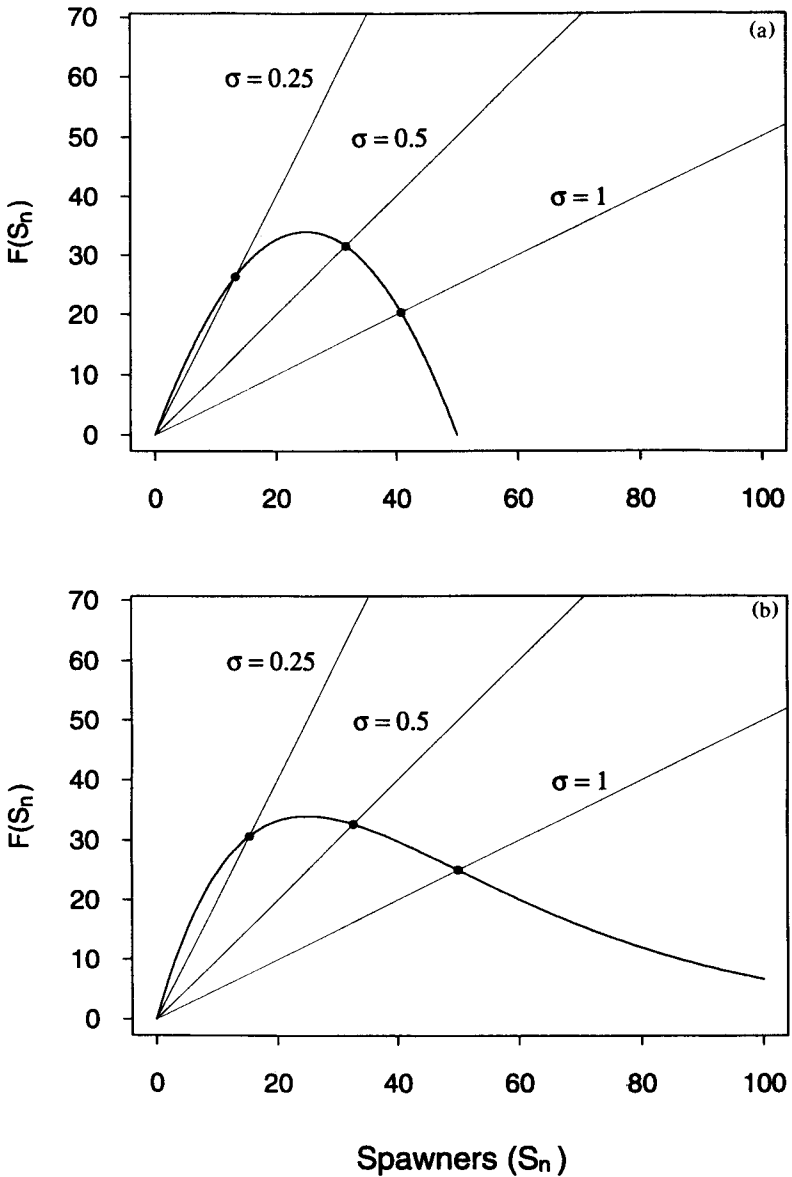


FIG. 1. Illustration of two overcompensatory stock-recruitment curves with the replacement lines and corresponding equilibria (heavy dots) for three values of the spawners-per-recruit parameter σ . (a) The logistic stock-recruitment curve, which is parabolic; (b) the Ricker stock-recruitment curve, $F(S_n) = \alpha S_n \exp(-\beta S_n)$. The numbers on the axes are arbitrary but could be in units of hundreds of whales, millions of fish, etc.

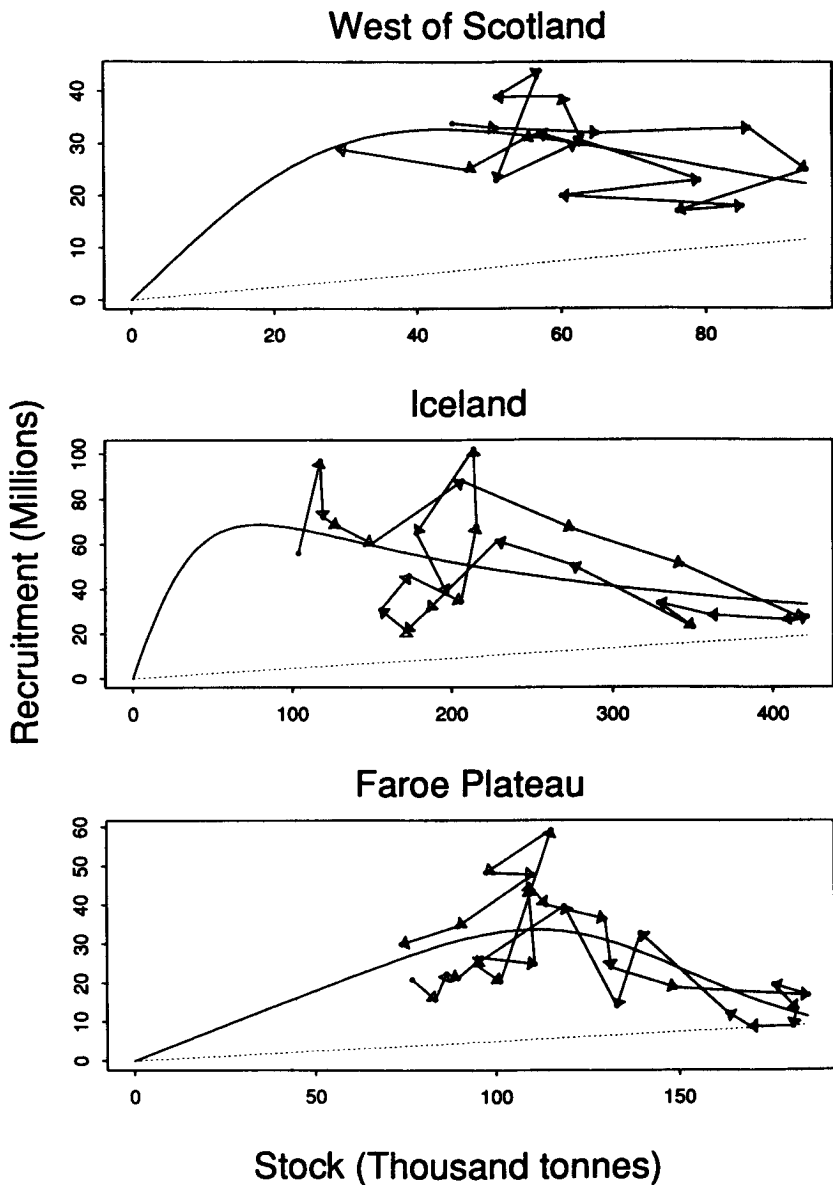


FIG. 2. Stock–recruitment trajectories and fitted Shepherd functions (Section 2.3) for three saithe stocks (data from the database described in Myers et al. [6]). Points on the stock–recruitment trajectories are separated by 1 year. Recruitment is given in numbers of 3-year-olds, and the spawning stock is given in terms of biomass, following fisheries convention, rather than numbers of spawners. The dotted line is the replacement line for zero harvest rate (all mortality is natural).

function F . Specifically, consider the example of a Ricker form (Figure 1) for year class strength:

$$F(S_n) = \alpha S_n \exp(-\beta S_n),$$

so that $\tilde{F}(S_n) = -\alpha_* S_n \exp(-\beta S_n)$, where α_* ($= \sigma\alpha$) is a function of σ . Thus, σ cannot be eliminated from the population dynamics; this will be further elaborated in Section 2.3.

2.1. STABILITY ANALYSIS

We follow the standard procedure of analyzing the stability of equilibrium (4) when it is subjected to small perturbations (s_n) about equilibrium. We write

$$S_n = S_0 + s_n, \quad F_n = F_0 + F'_0 s_n, \quad F'_0 \equiv \left[\frac{dF(S_n)}{dS_n} \right]_{S_n=S_0}. \quad (5)$$

We now substitute the expressions in (5) into (3) to obtain the governing equation for the linearized dynamics:

$$s_n = l s_{n-1} + \sigma F'_0 s_{n-k}. \quad (6)$$

By making the substitution $s_{n+k} = \chi^k s_n$, Equation (6) can be rewritten as an algebraic equation (the characteristic equation) in χ :

$$\chi^k - l\chi^{k-1} - \sigma F'_0 = 0. \quad (7)$$

The roots of this polynomial characterize the response of the stock to small perturbations about equilibrium. These roots are in general complex. If $|\chi| < 1$, then the trajectory is stable, consisting of either a monotonic approach to equilibrium (for χ real and positive) or damped oscillations (for χ complex or real and negative). If $|\chi| > 1$, then the trajectory is unstable, consisting of either monotonic growth (for χ real and positive) or growing oscillations (for χ complex or real and negative). It is clear from (7) that stability depends on both l and σ .

2.2. RICKER OSCILLATIONS

Although the stability properties of the Clark-type models with overcompensatory stock-recruitment relations have been quite thoroughly treated, there has been less attention to the periods of the oscillations predicted by these models. Ricker [7] was the first to note long-period endogenous population fluctuations, which appeared in his simulations of the population trajectory of an age-structured fish stock

with strong overcompensation in its (Ricker-type) recruitment function. Ricker estimated that the natural period of these oscillations is twice the median time from oviposition to oviposition (the time required for an egg to develop into a spawning fish). There is not general agreement [3] on the exact formulation for the period (say, time from oviposition to oviposition versus mean age of spawners), and this motivates us to examine the periods of the modes (particularly the unstable modes) of a Clark model in more detail. We will refer to the oscillations having a period associated with the time required for an animal to mature as Ricker oscillations.

A Clark model can reproduce Ricker oscillations. In the model specified by (7), results are very easily obtained when $l = 0$. In this case, the inequality $\sigma F'_0 < -1$ defines instability. With this specification, the k roots of (7), which we write as χ_m ($m = 1, 2, \dots, k$), are

$$\chi_m = e^{i\pi(1+2m)/k} |\sigma F'_0|^{1/k}, \quad m = 1, 2, \dots, k. \quad (8)$$

Each of the factors $\phi_m = \exp[i\pi(1+2m)/k]$ represents the oscillatory part of a root, and since $\phi_m^{2k} = 1$, the oscillation has period $2k$. This may be regarded as the simplest example of Ricker oscillations. (For k odd there is one root with a period of 2 years; this is discussed below.)

In Figure 3 we present polar plots of the roots of (7), for various values of l , for the case $\sigma F'_0 = -1$ (which represents neutral stability for $l = 0$). The roots were extracted using the algorithm described by Jenkins and Traub [8] with modifications of Withers [9]. In Figure 3 the vertical axis represents the imaginary part of the root and the horizontal axis represents the real part. Each root corresponds to a possible mode of oscillation, each with a characteristic frequency and damping or growth rate. The circle appearing in this figure, representing neutral stability, is defined by $|\chi| = 1$. Roots lying inside this circle represent a stable response to perturbations, and those found outside the circle represent unstable behavior. For $l = 0$ the root lies at the tail of the first arrow; for succeeding cases ($l = 0.2, 0.4, 0.6, 0.8$), the roots lie at the head of each arrow. For $l = 0$ the roots all lie on the circle of neutral stability. As l increases, the roots move either inside or outside the circle (or along the circle in the $k = 2$ case). The effect of l on stability has been discussed in some detail by Clark [1] and Botsford [3].

It is apparent from Figure 3 that, for the second-order (age at maturity $k = 2$) case, stability does not depend on l (this result is given in Clark [1]). For the higher order ($k > 2$) cases presented, there is a consistent pattern: The roots having the largest real part are found the furthest beyond the circle of neutrality, and thus these roots represent the most unstable modes. It is evident that increasing l decreases

stability; that is, the roots of the most unstable modes move further from the circle of neutrality (this was demonstrated by Clark [1]).

Previous studies have not noted the presence of roots on the negative real axis for the odd-order cases, corresponding to oscillations with a period of 2 years rather than the Ricker period of about $2k$ years. If all modes were stable, this 2-year oscillation (and other modes) could reach appreciable amplitude under driving by environmentally induced recruitment fluctuations, which would appear as a forcing term in (3) (and equations derived from it). For unstable conditions, the longer period modes will dominate because they have higher growth rates. There is some empirical evidence for a 2-year mode; Myers and Cadigan [10] found evidence for negative autocorrelation between adjacent cohorts (suggestive of a 2-year oscillation) for the North Sea cod (*Gadus morhua*) stock (these fish mature at 3 years of age). (Other interpretations of this feature are possible [10].)

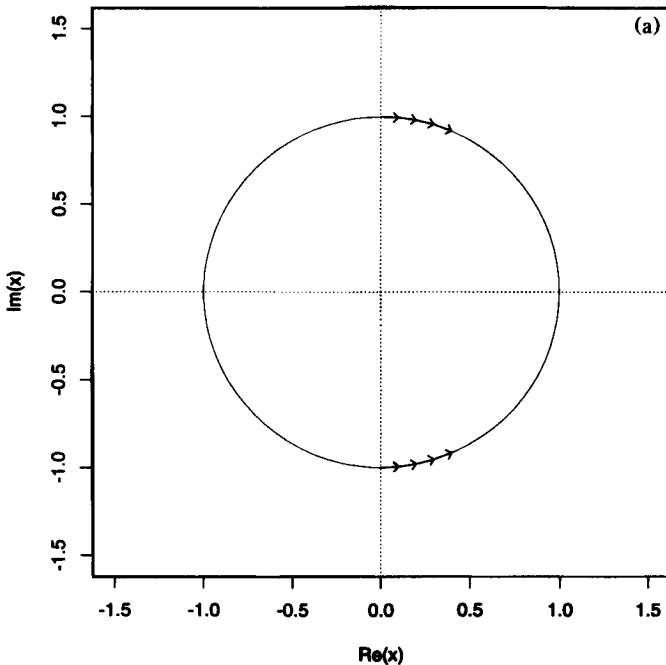


FIG. 3. The roots of the characteristic equation, Equation (7), plotted in the complex plane (imaginary part versus real part), for ages at maturity of (a) 2, (b) 3, (c) 4, (d) 5, (e) 6, (f) 7, and (g) 8. In each panel, for $l = 0$ the root lies at the tail of the first arrow; for succeeding cases ($l = 0.2, 0.4, 0.6, 0.8$) the root lies at the head of each arrow, with the arrows indicating the direction of increasing l . Points of neutral stability lie on the circle in each panel.

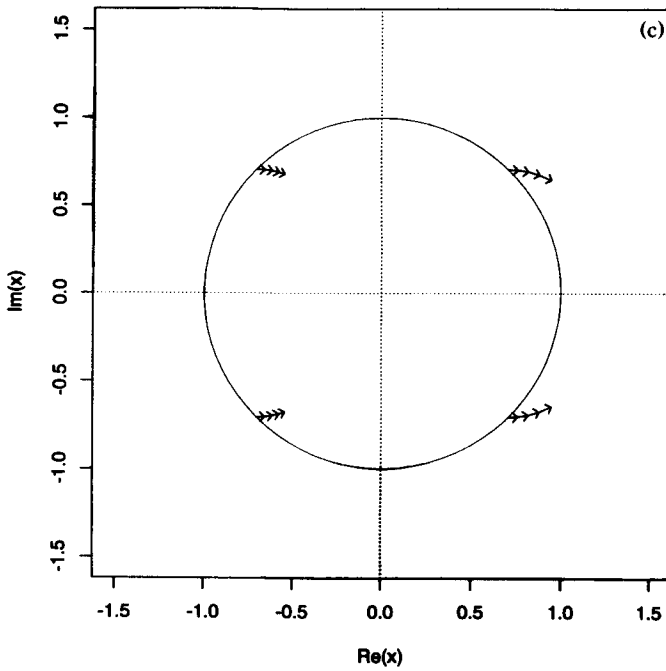
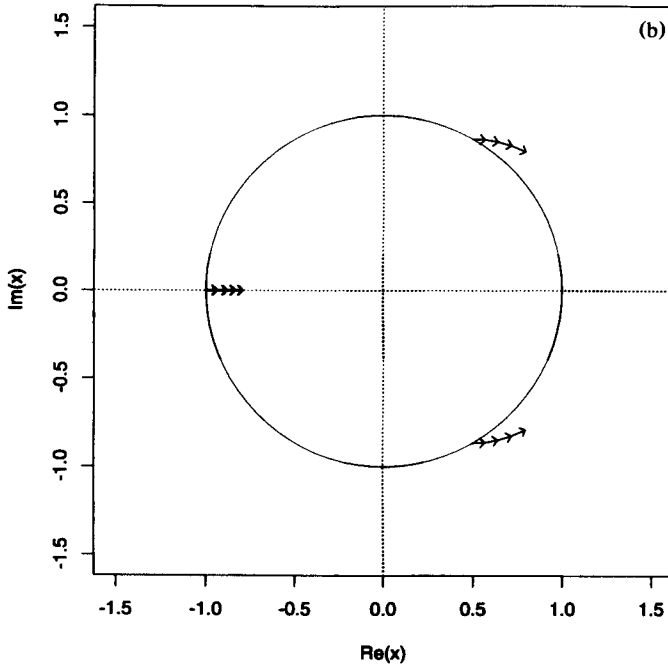


FIG. 3. (Continued)

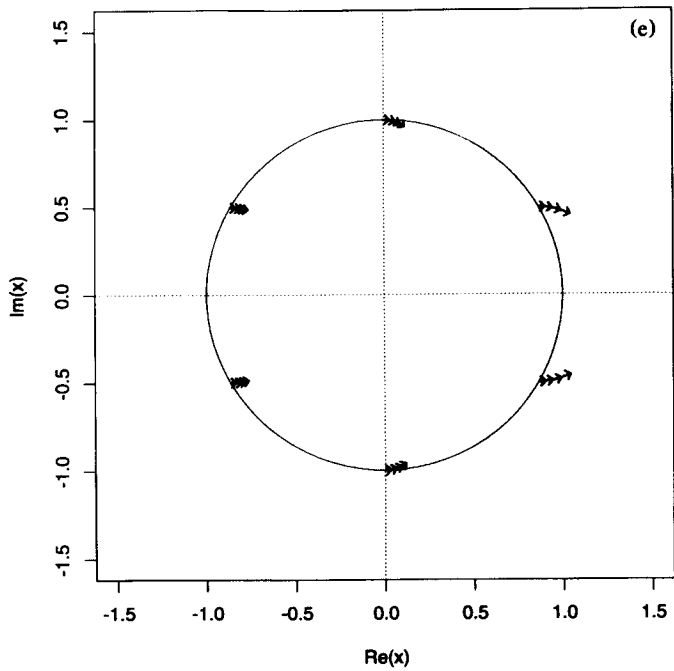
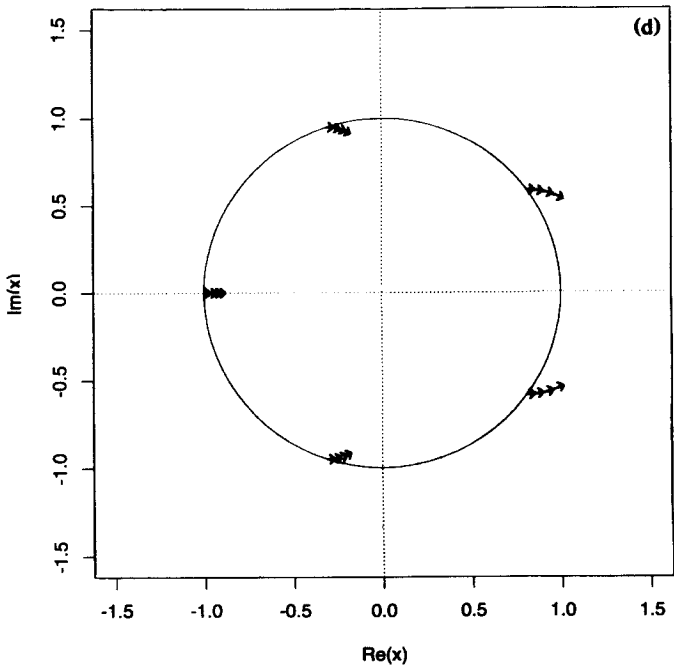


FIG. 3. (Continued)

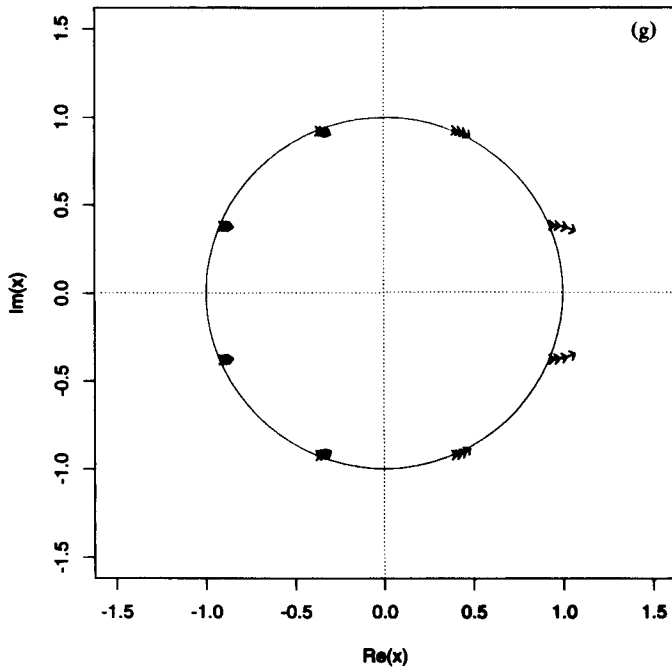
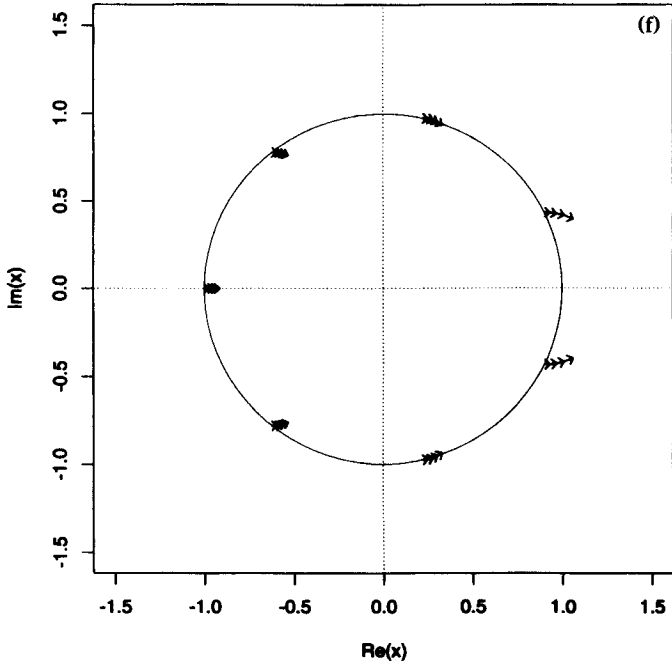


FIG. 3. (Continued)

The roots appear (Figure 3) as conjugate pairs, reflected through the real axis (except for the root on the negative real axis, which occurs for k odd). As l increases, the roots in the upper half-plane swing clockwise toward the positive real axis, and their reflections in the lower half-plane swing counterclockwise, again toward the positive real axis. These displacements correspond to increasing periods, as is readily demonstrated for the analytically tractable second-order ($k = 2$) case. The period T may be written as $2\pi/T = \theta$, where θ is the angle between the positive real axis and the line segment joining the origin and the root. For the $k = 2$ case it is easily shown that

$$T = 2\pi \left[\arccos \left(\frac{l}{2\sqrt{-\sigma F'_0}} \right) \right]^{-1} \approx 4 \left(1 - \frac{l}{\pi\sqrt{-\sigma F'_0}} \right)^{-1}. \quad (9)$$

The approximation in (9) is accurate to within about 1% for $-\sigma F'_0 \approx 1$ and $0 \leq l \leq 0.8$. It is clear that T increases as l increases. From (9), the period of the oscillations for the $k = 2$ case in Figure 3 varies from 4 years ($l = 0$) to 5.4 years ($l = 0.8$). For $k > 2$ the displacements of the roots with increasing l are smaller than those apparent for the $k = 2$ case; for the $k = 8$ case the period of the most unstable root in Figure 3 varies from 16 years ($l = 0$) to 19.8 years ($l = 0.8$). The periods of the Ricker oscillations are not strongly dependent on l .

Botsford [3] has summarized earlier work giving estimates of the natural period of endogenous (Ricker-type) population oscillations. It has been contended by some authors that the fundamental period is twice the mean age of mature animals, this latter quantity being given by $T_m = k + l/(1-l)$. Botsford notes that numerical results indicate that the endogenous population oscillations do not have a period equal to twice the mean age of mature animals. For $k = 2$, $2T_m = 4\{1 + l/[2(1-l)]\}$, verifying [compare with (9)] that there is no simple relationship between the natural period of these population oscillations and twice the mean age of mature animals. Moreover, the appearance of the term $\sigma F'_0$ in formula (9) for the period shows that this period cannot be equal to the time from oviposition to oviposition (which is a trait of individual fish, whereas $\sigma F'_0$ is a characteristic of the population).

2.3. STABILITY AND HARVEST POLICY

Our generalization of the Clark model, the inclusion of the spawners-per-recruit parameter, is essential to understanding aspects of the influence of harvest policy on stability. Stability may be affected by managed changes in overall fishing mortality (discussed by Goh and Agnew [2]), but also by more specific changes, such as in targets for numbers of spawners per recruit (perhaps through adjustment of mesh

size regulations in a fishery). Equation (7) allows a ready appraisal of these effects.

There are several possible selections for the stock–recruitment function. The logistic illustrated in Figure 1 was considered by Goh and Agnew [2] to be a plausible form. It may be dealt with in a purely graphical fashion. As shown in Figure 1, increasing σ pushes the equilibrium point toward the horizontal. For the logistic, which is parabolic, the slope of the stock–recruitment curve at equilibrium (F'_0) increases as the equilibrium point approaches the horizontal axis. The stability-determining term in (7) is $\sigma F'_0$ (regarding l as fixed), and it clearly increases with increasing σ , implying that improving the number of spawners per recruit (σ) tends to destabilize the stock.

The Shepherd function [11, 12], $F(S_n) = \gamma S_n / [1 + (S_n/K)^\delta]$, is a versatile three-parameter stock–recruitment relationship, and it is amenable to straightforward analysis. The equilibrium [Equation (4)], if it exists, is given by

$$S_0 = K \left[\frac{\delta\sigma}{1-l} - 1 \right]^{1/\delta}. \quad (10)$$

The stability-determining term, $\sigma F'_0$, for the Shepherd curve is, using (10),

$$\sigma F'_0 = (1-l) \left[(1-\delta) + \frac{(1-l)\delta}{\gamma\sigma} \right] \quad (11)$$

It is apparent from (11) that the effect of increasing σ is to push the stock toward instability, since the term guaranteed to be positive, $[(1-l)\delta/\gamma\sigma]$ (note that σ is taken to be positive), decreases when σ increases.

Alternatively, we could adopt a Ricker formulation for the recruitment function, again $F(S_n) = \alpha S_n \exp(-\beta S_n)$. Equilibrium [Equation (4)] is possible if $\alpha > (1-l)/\sigma$, and the equilibrium spawning stock is given by

$$S_0 = -\frac{1}{\beta} \ln \left(\frac{1-l}{\alpha\sigma} \right). \quad (12)$$

Using (12), we find

$$\sigma F'_0 = (1-l) \left[1 + \ln \left(\frac{1-l}{\alpha\sigma} \right) \right] = (1-l)(1 - \beta S_0). \quad (13)$$

As was true for the Shepherd curve, Equation (13) shows that, for a Ricker function, increasing σ always tends to destabilize the stock

dynamics. [This is particularly clear from the second expression in (13), since S_0 must increase as σ increases].

For all three stock–recruitment functions considered, increasing the number of spawners per recruit is a destabilizing influence, provided that the stock–recruitment curves are domed. The Shepherd function appears to be general enough to provide acceptable fits to all extant stock–recruitment data exhibiting overcompensation [6]. Thus we claim that our results have broad applicability to fisheries.

This result may be compared with that found by Goh and Agnew [2]; they found that either high or low fishing mortalities could destabilize a stock having an overcompensatory stock–recruitment relation. This is readily understood by considering the replacement line for the equilibrium stock. At certain levels of fishing mortality the replacement line intercepts the stock–recruitment curve at a point where it has an appreciable negative slope. Increasing or decreasing the fishing mortality will alter the slope of the replacement line, shifting the point of intersection away from the point of greatest negative slope (of the stock–recruitment curve). In contrast, for our example, changing σ has a monotonic effect. Again, the slope of the replacement line will vary with σ (see Figure 1), with attendant changes in the slope of the stock–recruitment curve at the equilibrium point. However, the factor σ , appearing in the term $\sigma F'_0$ in Equation (7), ensures a monotonic tendency for increases in σ to destabilize the dynamics. Adjustments of harvest policy to increase the number of spawners per recruit will tend to have a destabilizing influence.

3. SUMMARY

We have presented a simple modification of the Clark model that allows for the demise of recruits before they become spawners. The spawners-per-recruit parameter has been shown to have a significant influence on population stability. When instabilities are present, our linear analysis has shown that the resulting oscillations tend to have a period that is slightly greater than twice the age of maturity. A management strategy targeted at increasing the number of spawners per recruit will tend to destabilize the stock, regardless of the initial number of spawners per recruit, when overcompensation occurs in the stock–recruitment function.

Finally, the model presented here lends itself to extension to stochastic fisheries problems (for a discussion of these, see, e.g., Fogarty et al. [13] or Sissenwine et al. [14]). In simulation treatments, stochasticity is often [7] introduced via multiplicative noise in the recruitment, that is, $F(S_{n-k}) \rightarrow F(S_{n-k}) \exp(\varepsilon_{n-k})$, where ε_{n-k} represents a zero-mean normally distributed random process. The model developed here permits

analysis of these problems in a format far simpler than fully age-structured models for which a large suite of parameters must be specified. Hilborn and Walters [15] have emphasized the desirability of formulating realistic population models for fisheries that incorporate only a small number of easily estimated parameters. The model elaborated here is apparently the simplest model that reproduces the frequency structure of population fluctuations (Ricker oscillations), and thus it is a plausible candidate for application to stochastic fisheries problems.

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