TIME-DEPENDENT SOLUTIONS AND EFFICIENT PARAMETERS FOR STOCK-PRODUCTION MODELS

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ABSTRACT

The time-dependent formulations of the Graham-Schaefer and Pella-Tomlinson systems are restructured so as to accommodate directly the critical-point parameters of their respective governing graphs; the resulting parametric system accounts for the behavior of either model wholly in terms of its management components. The indeterminate exponent and the coefficients of the Pella-Tomlinson equations are uncoupled and the dual formulations associated with the conventional casting of the system are eliminated; the governing equations and corresponding solutions are cast into composite forms and the sign changes of coefficients become automatic. The previously obscure relationships between management parameters and variable graph curvature in the Pella-Tomlinson model are expressly formulated; maximum sustainable yield is shown to be independent of the indeterminacy of the system. Time-delay estimators for both systems are formulated.

We analyze here, in a deterministic setting, certain of the transient, nonlinear mechanisms employed in the modelling of stock and yield during periods of imbalance between fishing removals and stock productivity. The general method of analysis, which appeals primarily to the direct parameterization of critical points, will apply to any nonlinear scheme of exploitation and gross production, but it applies in particular to the Graham-Schaefer hypothesis (Graham 1935; Schaefer 1954) and to the "generalized" model of Pella and Tomlinson (1969). Since control of either system rests ultimately with the control of critical points, we restructure the parametric definitions accordingly and the governing equations for both systems are then controlled directly by parameters of management significance.

Typically, either system reflects the deterministic premise that a stock of fishes, otherwise held by exploitation at levels below a prior abundance, will constantly strive to recover its numbers in accord with some innate, self-regulating, and repeatable mechanism of restoration. Any such restoration must accrue from the productivity of the stock, and by Graham's hypothesis, the inherent or latent capacity for productivity in a stock of fishes depends jointly on the current size of the stock (in numbers or biomass) and the difference between the current and potentially maximum sizes. Whence, in terms of time-dependent biomass B, and with the proportionality coefficient defined as the ratio of "intrinsic" growth rate k and b_∞, Graham's formula for latent productivity $\dot{P}$ takes on the familiar form

$$\dot{P}(B) = kB - \frac{k}{B_\infty} B^2. \tag{1}$$

Of the two expanded terms, the first governs the intrinsic, exponential capacity for growth of the population's biomass, while the negative, nonlinear term provides the damping that ultimately slows growth as $B(t)$ approaches its asymptotic maximum B_∞. The two terms, in their algebraic sum, govern the latent productivity of the stock at any stock size between zero and B_∞. Parameter k, as we shall see, is coupled analytically and phenomenologically to parameter B_∞, but the dependence of k on root B_∞ in Equation (1) can be supressed in favor of the direct parameterization of maximum productivity (which, in the complete exploitation model, we identify with maximum yield rate).

In the Pella-Tomlinson model, the parametric controls for latent productivity exceed by one the total number of such parameters in Graham's formulation, an increase in freedom that comes at considerable cost to tractability, both analytical and statistical. The differential equation that governs latent productivity in the Pella-Tomlinson system has the indeterminate form

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$$\dot{P}(B) = c_1B + c_2B^n, \qquad (2)$$

with exponent n the additional parameter, but with the signs of the coefficients now dependent on the range of definition of n. As before, the combined terms describe, at any stock size B, the stock's latent capacity for productivity. With n undetermined (its determination being a part of the empirical demonstration), solutions of Equation (2) constitute infinitely many growth laws. By setting $n = 2$, and with $c_1 > 0$, $c_2 < 0$, Equation (2) reduces to the Graham equation (Equation (1)). Pella and Tomlinson (1969) attribute Equation (2) to Richards (1959). For a detailed analysis of (2) as a general growth form, see Fletcher (1975); the anticedents of this analysis appear there.

In either of the two systems, exploitation enters the formulation for productivity by the direct difference $\dot{P} - \dot{Y}$, with $\dot{Y}$ signifying the rate of biomass removal owed to exploitation and $\dot{P}$ the latent productivity of the stock. Wherefore, in writing

$$\dot{B}(B) = \dot{P}(B) - \dot{Y}(B), \qquad (3)$$

we interpret $\dot{B}(B)$ as being the resultant productivity, at stock size B, that nets to the stock for its growth. The net may be positive, negative, or zero accordingly as $\dot{P}$ and $\dot{Y}$ vary with B. That is

> $\dot{P} > \dot{Y}$ implies $\dot{B} > 0$: the stock's latent productivity exceeds the rate of exploitation; a positive net productivity remains to the stock and the stock so tends to a higher level of biomass.
>
> $\dot{P} < \dot{Y}$ implies $\dot{B} < 0$: the rate of biomass removal exceeds the stock's capacity for growth; the stock adjusts to the deficit in net productivity by tending to a lower level of total biomass.
>
> $\dot{P} = \dot{Y}$ implies $\dot{B} = 0$: the exploitation rate just balances latent productivity, and biomass trajectory $B(t)$ exhibits an extremum. Should $\dot{B} = 0$ over finite time, stock biomass remains stationary and the state called "equilibrium" prevails.

Although the detailed time course of any real stock biomass is actually determined by variations in renewal, survival, member growth, and the age- or size-dependent probabilities of capture, such effects are not usually separated in the models of interest here, and yield rate $\dot{Y}$ customarily takes the form

$$\dot{Y}(t) = F(t) \cdot B(t), \qquad (4)$$

with the implication that all fish of the fishable stock are presumed to share, in equal measure, the force of fishing mortality F, irrespective of age or size. By admitting Equation (4) into Equation (3), our general form for net productivity becomes

$$\dot{B} = \dot{P} - F \cdot B, \qquad (5)$$

where the time variation of F is usually prescribed by average effort f on the assumption that $F = qf/\tau$, quantity q being the individual probability of capture per unit of effort and τ the averaging interval measured in fractions of the dimensional time unit of F.

ANALYSIS OF THE GRAHAM SYSTEM

Figure 1 illustrates the phase-plane graph of Equation (1), the latent productivity of a Graham stock. Maximum productivity m occurs at stock size p. And regardless of the conventions employed in the formulation of Equation (2), essential parametric control in the equation resides specifically with its nonzero root B_∞ and with coordinate m of the critical point (p, m). Parameter m and B_∞ constitute a complete, minimum set of analytically independent parameters for latent

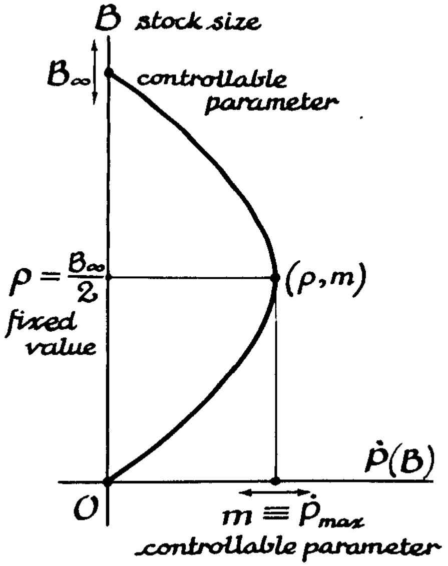


FIGURE 1.—Latent productivity $\dot{P}$ as a function of stock size B, the Graham model. See Equations (1) and (1a).

productivity in the Graham system, and they represent the whole extent of available control over the graph of Equation (1). Coordinate p of the critical point has the fixed value $B_\infty/2$, and the graph of Equation (1) has a fixed curvature of second degree.

Wherefore, productivity Equation (1), cast directly in terms of analytical parameters m and B_∞, takes on the form

$$\dot{P} = 4m\left[\frac{B}{B_\infty}\right] - 4m\left[\frac{B}{B_\infty}\right]^2, \tag{1a}$$

and intrinsic rate k, as it turns out, bears a proportionality dependence on maximum productivity and maximum biomass in the relationship

$$k = \frac{4m}{B_\infty}\left[\equiv 4\frac{P_{\max}}{B_{\max}}\right]$$

And with the substitution of Equation (1a) into Equation (5), the formula for the net productivity of a Graham stock becomes

$$\dot{B} = 4m\left[\frac{B}{B_\infty}\right] - 4m\left[\frac{B}{B_\infty}\right]^2 - FB. \tag{6}$$

In the integrated, equilibrium versions of the Graham system, maximum latent productivity m becomes maximum sustainable yield (MSY), hence parameter m may be directly interpreted as MSY in any optimization procedure on Equation (6).

If we restrict the time-dependence of F to abrupt changes so that any solution of Equation (6) corresponds on its interval of validity, however brief, to some constant value of F, then the time-dependence of B in Equation (6) becomes

$$B(t) = \frac{B_*}{1 + C_0 e^{-(4m/B_\infty - F)t}} \qquad B_* = \left[1 - \frac{FB_\infty}{4m}\right] B_\infty, \tag{7}$$

and with initial time t_0 set arbitrarily to zero, the integration constant in Equation (7) becomes

$$C_0 = \frac{B_* - B_0}{B_0}.$$

Figure 2 illustrates the relationship between net productivity (Equation (6)) and the biomass solution (Equation (7)) for cases where

$$F < \frac{4m}{B_\infty}.$$

As indicated in the figure, root B_* becomes the adjustment level to which biomass trajectory $B(t)$ will trend when F is less than critical quantity $4m/B_\infty$ (and obviously, $B(t)$ trends to B_∞ in Equation (7) when F is zero). The system is governed by the positive branch of Equation (6) when $\dot{Y} < \dot{P}$ (in which case, $\dot{B} > 0$), and by the negative branch of Equation (6) when $\dot{Y} > \dot{P}$ (in which case, $\dot{B} < 0$). But this partitioning of F into subranges for negative or positive $\dot{B}$ is a density-dependent process. Although we must have $F < 4m/B_\infty$ for positive B_*, the values of F on that range that drive the stock either up or down will depend on initial stock size B_0. To insure, for arbitrary B_0, that $\dot{Y} < \dot{P}$ in Equation (6), mortality F must have a value such that

$$0 < F < \frac{4m}{B_\infty}\left[1 - \frac{B_0}{B_\infty}\right],$$

in which case $B(t)$ increases from initial value B_0 towards a higher adjustment level B_*. But for any value of F on the interval

$$\frac{4m}{B_\infty}\left[1 - \frac{B_0}{B_\infty}\right] < F < \frac{4m}{B_\infty},$$

then $\dot{Y} > \dot{P}$ and $B(t)$ decreases from B_0 towards a lower adjustment level B_*.

Figure 3 illustrates the relationship between net productivity (Equation (6)) and the biomass solution (Equation (7)) when

$$F \geq \frac{4m}{B_\infty},$$

in which case the adjustment level of biomass corresponds to the zero root of Equation (6). As indicated by the figure, any mortality F so great as to equal or exceed the quantity $4m/B_\infty$, if maintained, will fish a Graham stock to extinction.

Since Equation (6) governs the relationship between transient biomass and nonequilibrium removal, we look to its solution (Equation (7)) for time delays between equilibria. But the asymptotic behavior of Equation (7) is a minor analytical annoyance to be circumvented here. Let us

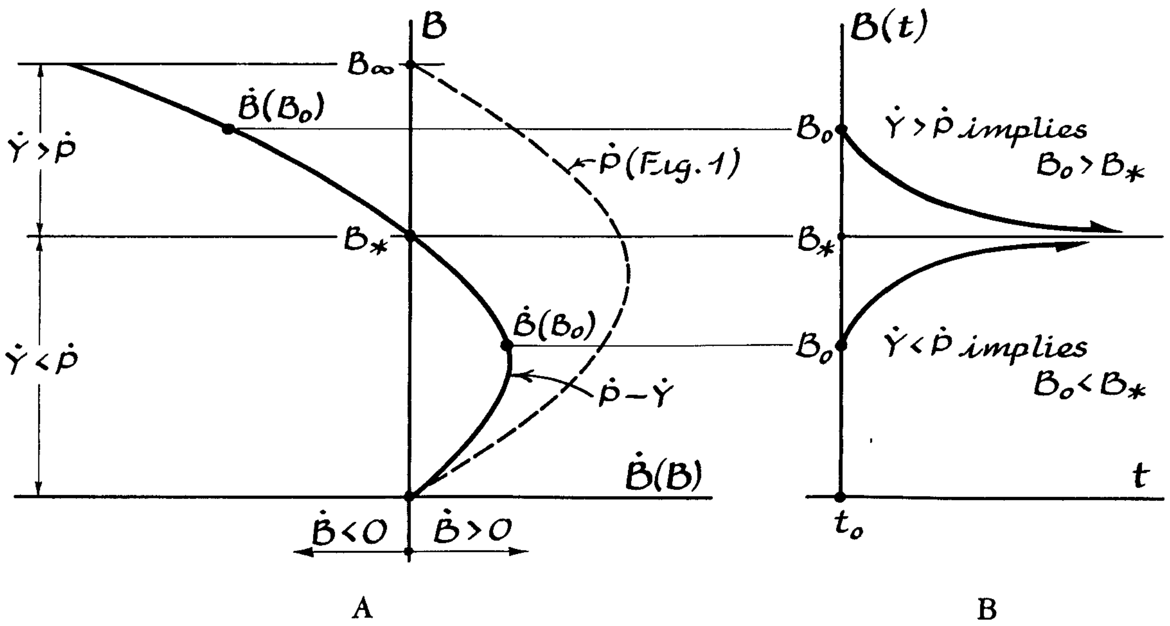


FIGURE 2.—A. Typical phase-plane graph of net productivity $\dot{B} = \dot{P} - \dot{Y}$, Equation (6), the Graham system, with mortality F constrained to the interval $0 < F < 4m/B_\infty$. When removal rate $\dot{Y}$ exceeds latent productivity $\dot{P}$ then $\dot{B} < 0$ and the negative branch of Equation (6) applies. When productivity $\dot{P}$ exceeds removal rate $\dot{Y}$ then $\dot{B} > 0$ and the positive branch applies. B. Typical solution graphs of stock biomass $B(t)$, Equation (7). When $\dot{Y} > \dot{P}$, biomass declines from initial value B_0 towards adjustment level B_*. When $\dot{Y} < \dot{P}$, biomass increases from initial value B_0 towards adjustment level B_*.

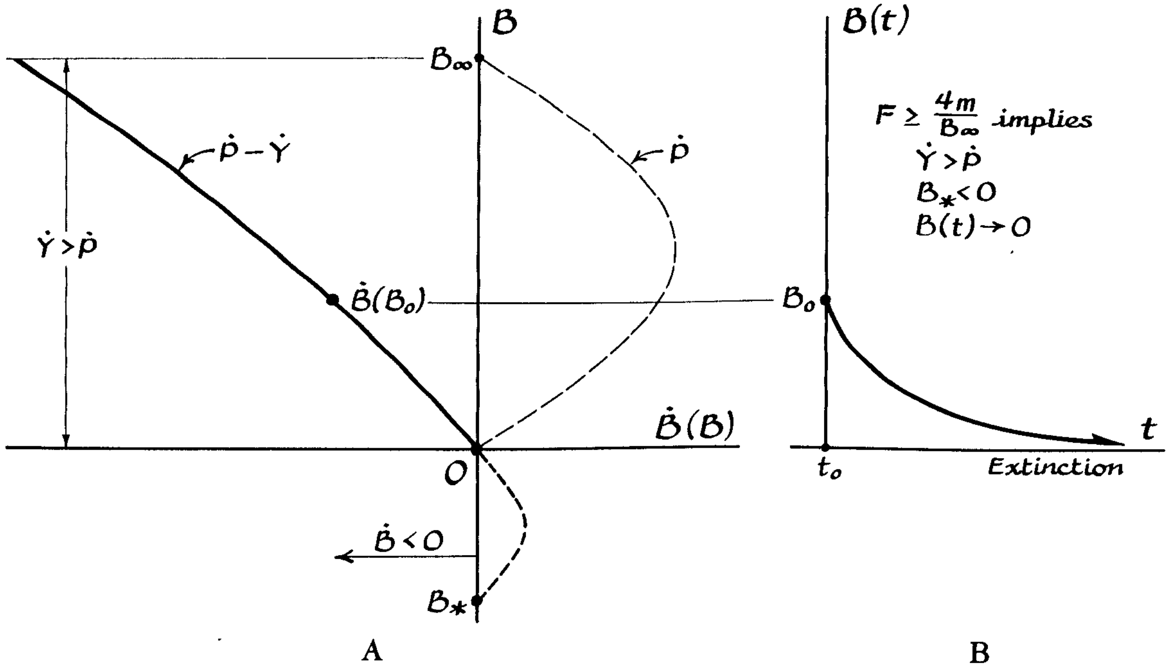


FIGURE 3.—A. Typical graph of net productivity $\dot{B} = \dot{P} - \dot{Y}$, Equation (6), the Graham system, with mortality $F \geqslant 4m/B_\infty$. For any such value of F, the zero root of Equation (6) applies, removal rate $\dot{Y}$ exceeds latent productivity $\dot{P}$, and $\dot{B} < 0$. B. Typical solution trajectory $B(t)$ of Equation (7) when $F \geqslant 4m/B_\infty$. Biomass declines from initial value B_0 towards extinction level $B = 0$.

presume that no practical technique of estimation will have a precision of resolution better than some assignable percentage of true stock size, and let us reflect that practical uncertainty in our analysis by expanding the asymptotic bound of Equation (7) to a region of radius $\epsilon \cdot B_*$ around the analytical value of the bound (ϵ being the measure of the uncertainty). Whence, with B_0 and B_1 now signifying initial and adjustment levels, and by supposing that F changes abruptly at time t_0 from value F_0 to some new value F_1, Equation (7) becomes

$$(1 \pm \epsilon) = \frac{1}{1 + C_0 e^{-(4m/B_\infty - F_1)t}},$$

the plus sign applying when $F_1 > F_0$ and the minus sign when $F_1 < F_0$. By setting initial time t_0 arbitrarily at zero,

$$C_0 = \frac{B_1 - B_0}{B_0},$$

and the transition time between initial level B_0 and the ϵ-region at adjustment level B_1 becomes

$$t_{\text{lag}} = \frac{1}{4m/B_\infty - F_1} \ln \left[\frac{(1 \pm \epsilon)(B_1 - B_0)}{-(\pm \epsilon B_0)} \right]. \tag{8}$$

In few commercial fisheries do we expect to see exploitation rates constant over intervals equal to transition times t_{lag}, and in any case we anticipate considerable variation in stock size along the way, owing to chance events. Nevertheless, Equation (8) serves a purpose; it will give us some idea, in a management strategy, of the time delays to be expected in bringing a stock from one general state of exploitation to another through the regulation of mortality F.

To illustrate the particularization of Equation (8), we follow an adaptation by Ricker (1975: 312-315) of Graham's work on demersal stocks of the North Sea. To accommodate our formulation here, parameters for Ricker's adaptation would be

B_∞ = 220,000 tons,
m = 40,300 tons yr^{-1} (the MSY of the model).

With reference to Ricker's illustrations (1975: 312-315), we first calculate the time delay that accompanies a reduction in mortality from F_0 = 0.40 yr^{-1}, corresponding to a stock level of B_0 = 100,000 tons, to a new mortality commencing at reference time zero, of F_1 = 0.20 yr^{-1}. The adjustment level to which $B(t)$ will trend in the transition period is B_1 = 160,000 tons (by setting, in Equation (6), $\dot{B} = 0$, $F = F_1$ and $B = B_1$. If we now specify the uncertainty in estimation precision as being, say, 5% of true stock size, then Equation (8), with $F_1 < F_0$ and $\epsilon = 0.05$, gives the estimated delay in adjustment as

$$t_{\text{lag}} = \frac{1}{0.533} \ln \left[\frac{(1 - 0.05)\,(160{,}000 - 100{,}000)}{0.05(100{,}000)} \right]$$
$$= 4.6 \text{ yr.}$$

When the model stock declines between similar levels, the time delay is longer. That is, stock at level B_0 = 160,000 tons, corresponding to the fishing mortality F_0 = 0.20 yr^{-1}, declines to the adjustment level B_1 = 100,000 tons following an increase at $t_0 = 0$ to the new mortality F_1 = 0.40 yr^{-1}. Transition time t_{lag} now becomes

$$t_{\text{lag}} = \frac{1}{0.333} \ln \left[\frac{(1 + 0.05)\,(100{,}000 - 160{,}000)}{-0.05(160{,}000)} \right]$$
$$= 6.2 \text{ yr.}$$

Yields from transient periods differ considerably from the removals associated with equilibrium states. Obviously, an increase in fishing mortality increases the yield temporarily, and a decrease in fishing mortality decreases the yield temporarily, but the ensuing trends of adjustment will depend, in the context of the Graham system, on the following relationships:

$F < 4m/B_\infty$; stock size $B(t) \to B_*$ (Figure 2), which implies that $\dot{Y} \to FB_*$.

$F \geq 4m/B_\infty$; root $B_* < 0$ and $B(t) \to 0$ (Figure 3) which implies that $\dot{Y} \to 0$.

$F = 2m/B_\infty$; stock size $B(t)$ implies p (p being the biomass level $B_\infty/2$ where maximum latent productivity occurs; Figure 1), which implies that $\dot{Y} \to m$. Accordingly, we may identify parameter m, in any of the rate equations here, with MSY (which, we should remember, is itself a yield rate).

Since, by Equation (4), instantaneous removal varies in time as $\dot{Y}(t) = F(t)B(t)$, then over the course of the adjustment interval that follows an abrupt change in F, yield from a Graham stock will accumulate as

$$Y(t) = (B_\infty - B_*) \ln \left[1 + \frac{B_0}{B_*}\left(e^{(4m/B_\infty - F)t} - 1\right)\right] \tag{9}$$

$$B_* = \left[B_\infty - \frac{F B_\infty{}^2}{4m}\right].$$

ANALYSIS OF THE PELLA-TOMLINSON SYSTEM

As noted in the foregoing section, the maximum latent productivity m of a Graham stock always occurs at a biomass value exactly one-half the unexploited maximum B_∞. In turn, MSY of the equilibrium model must also occur at the stock level $B_\infty/2$. So as to gain control over the locations of those extrema, Pella and Tomlinson (1969) modify the Graham system by writing the differential equation for latent productivity $\dot{P}$ essentially in the form of Equation (2), which, by the customary treatment, has a troublesome, dual formulation owing to the sign changes at $n = 1$ of coefficients c_1, c_2. On the interval $0 < n < 1$ latent productivity in the Pella-Tomlinson system takes the basic form

$$\dot{P} = aB^n - bB \tag{10}$$

(where, for the sake of emphasis, $c_1 = -b$, $c_2 = a$, with a and b positive), but on the interval $n > 1$ latent productivity takes on the basic form

$$\dot{P} = bB - aB^n \tag{11}$$

(where $c_1 = b$, $c_2 = -a$, with a and b positive). In either case, the bound B_∞, the maximum productivity m, and the ordinate p (which governs the biomass level where m occurs), all depend on the numerical value assigned to exponent n. That is, root B_∞ is given by

$$B_\infty = \left[\frac{a}{b}\right]^{1/(1-n)},$$

the ordinate p is determined by

$$p = \left[\frac{an}{b}\right]^{1/(1-n)},$$

while maximum productivity m, by the conventional casting of the model, must be determined from the formula

$$^{\infty}m = \pm\,\frac{b(1-n)}{n}\left[\frac{an}{b}\right]^{1/(1-n)},$$

the plus sign applying to Equation (10) and the minus sign to Equation (11).

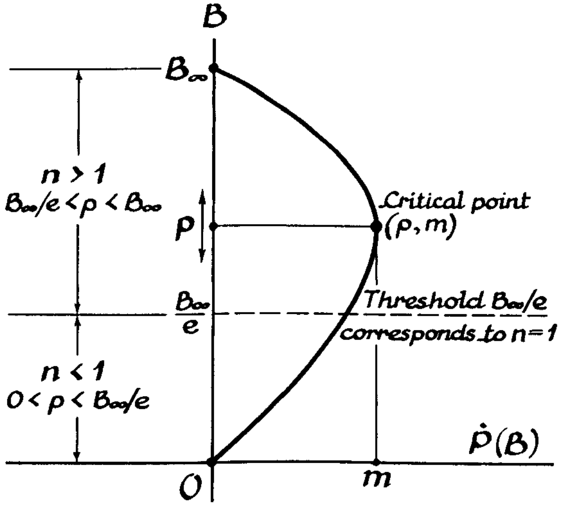


FIGURE 4.—Typical graph of Equation (12), latent productivity $\dot{P}$ as a function of stock size B, the Pella-Tomlinson system.

Coordinate p, in its location with respect to root B_∞, directly reflects the value assigned to exponent n, as indicated by Figure 4. When n takes any value between zero and unity, coordinate p falls on the range between zero and B_∞/e ($\approx 0.3679\,B_\infty$), in which case Equation (10) applies. When n takes any value greater than unity, coordinate p falls on the range between B_∞/e and B_∞, in which case Equation (11) applies. But the coordinate m has no essential dependence on exponent n, and its apparent coupling with n (as indicated by the formulation above) is merely an inconvenient artifact of the conventional analysis. With parameters m and n uncoupled (see Fletcher 1975), the Equations (10) and (11) that govern latent productivity in the Pella-Tomlinson system can be consolidated into the single governing equation

$$\dot{P} = \gamma m\left[\frac{B}{B_\infty}\right] - \gamma m\left[\frac{B}{B_\infty}\right]^n, \tag{12}$$

with γ a purely numerical factor wholly prescribed by n as

$$\gamma = \frac{n^{n/(n-1)}}{n-1}. \tag{13}$$

With the coefficients so cast, the sign reversals at turning point $n = 1$ become automatic. In consequence, the consolidated interval of definition for n becomes $0 < n < \infty$ (the point $n = 1$ being a removable singularity). With parameter m thus separated from n in Equation (12), the undetermined exponent n can be defined solely by the fraction p/B_∞ in the relationship

$$\frac{p}{B_\infty} = n^{1/(1-n)}. \tag{14}$$

Consolidated Equation (12) now takes on the role in the Pella-Tomlinson system that Equation (1a) takes on in the Graham system. In fact, when $n = 2$, Equation (12) reduces to Equation (1a), in which case $\gamma = 4$ and $p/B_\infty = ½$. As an interesting aside here, we note that Equation (12), at the turning point $n = 1$, takes on the form

$$\dot{P} = -e\,m \left[\frac{B}{B_\infty}\right] \ln \left[\frac{B}{B_\infty}\right]$$

(e being Napier's constant), while ratio (14), in the limit as $n \rightarrow 1$, has the value

$$\frac{p}{B_\infty} = \frac{1}{e}.$$

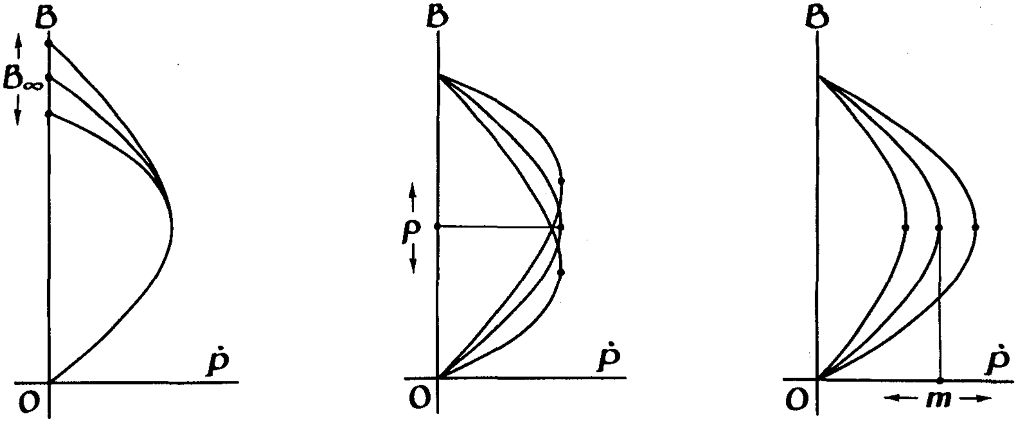
In fact, Fox (1970) constructed a stock-production model around this special case, but since the ratio p/B_∞ has the fixed value $1/e$, Fox's model "has as rigid a form as the Graham model" (Ricker 1975: 331).

Quantities m, p, and B_∞ constitute a complete, minimum set of independent parameters for latent productivity in the Pella-Tomlinson system. Collectively they control the behavior of governing Equation (12), but the influence of any one parameter remains independent of the remaining two. Figure 5 illustrates their separate effects on the graph of Equation (12).

By appealing to the same piecewise constraints that enter the Graham productivity equations, we substitute Equation (12) into the general productivity formula (Equation (5)) and net productivity in the Pella-Tomlinson system becomes

$$\dot{B} = \gamma m \left[\frac{B}{B_\infty}\right] - \gamma m \left[\frac{B}{B_\infty}\right] - FB. \tag{15}$$

And over any time interval, however brief, that mortality F might be presumed to have a fixed value, biomass variable B in Equation (15) has the general time-dependent solution



B_∞: unexploited stock level [the nonzero root of Equation (12)].

p: biomass level for maximum productivity [the coordinate of B in Equation (12) where m occurs].

m: maximum productivity [the extremum coordinate P_{max} in Equation (12)].

FIGURE 5.—The graph of Equation (12), latent productivity in the Pella-Tomlinson system, as controlled by independent parameters m, p, and B_∞.

$$B(t) = \left[B_*^{\,1-n} + C \exp\left((\gamma m/B_\infty - F)(1-n)\,t\right)\right]^{1/(1-n)}, \tag{16}$$

$$B_* = \left[\frac{\gamma m}{\gamma m - F B_\infty}\right]^{1/(1-n)} B_\infty.$$

By setting initial time t_0 arbitrarily at zero, the integration constant C in Equation (16) becomes

$$C = B_0^{\,1-n} - B_*^{\,1-n}.$$

Biomass Equation (16) will apply immediately upon a change in F and remain valid thereafter for the time that F remains constant. Over such time, population biomass will trend up or down in accord with Equation (16) from initial size B_0 towards adjustment level B_*. Should nonzero root B_* be negative (which is possible only when $n > 1$), then the adjustment level corresponds to the zero root of Equation (15) and the population tends to extinction by Equation (16).

The critical relationships between fishing mortality, productivity, and time-dependent yield rate in the Pella-Tomlinson system are considerably more complex than the relationships between F, $\dot{P}$, and $\dot{Y}$ in the Graham system. Figure 6 illustrates the behavior of $\dot{P} - \dot{Y}$ when $n < 1$, and Figures 7 and 8 illustrate $\dot{P} - \dot{Y}$ when $n > 1$. The ratio $\gamma m/B_\infty$ becomes the critical quantity in the Pella-Tomlinson system ($4m/B_\infty$ being its counterpart in the Graham system).

As indicated by Figure 6, the biomass level p where maximum productivity occurs must lie on the range $0 < p < B_\infty/e$ when $0 < n < 1$. And when n takes any such value, the corresponding Pella-Tomlinson stock will exhibit nonzero adjustment levels of biomass for all values of fishing mortality however large; such a stock cannot be fished to extinction. That is, nonzero root B_* of Equation (15) will always have a positive value when $0 < n < 1$, its range of variation being $0 < B_* \leq B_\infty$ for F unrestricted on $0 \leq F < \infty$. But F is partitioned into subranges accordingly as $\dot{Y} < \dot{P}$ or $\dot{Y} > \dot{P}$. And those values of F, for which $B(t)$ either increases or decreases to B_*, depend on the critical ratio $\gamma m/B_\infty$ and initial biomass value B_0. To insure, for arbi-

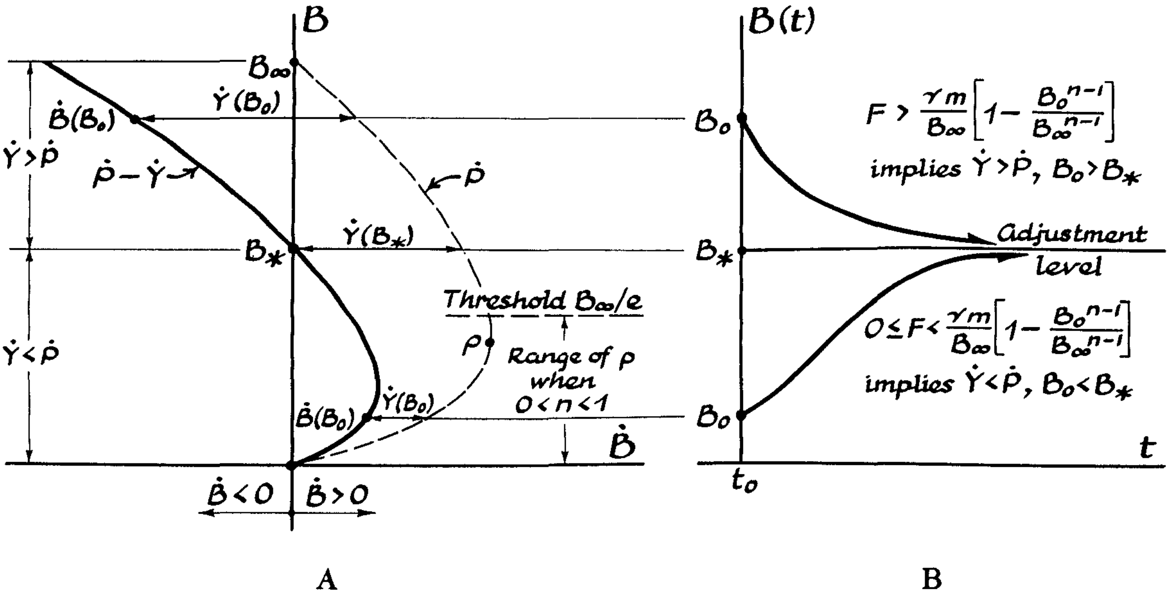


FIGURE 6.—A. Typical phase-plane graph of net productivity Equation (15), the Pella-Tomlinson system, for values of n where $0 < n < 1$. For any such value of n, root B_* of Equation (15) is always positive irrespective of the magnitude of F. Should removal rate $\dot{Y}$ exceed latent productivity $\dot{P}$, then $\dot{B} < 0$ and the negative branch of Equation (15) applies. Should $\dot{P}$ exceed removal rate $\dot{Y}$, then $\dot{B} > 0$ and the positive branch applies. B. Typical solution graphs of stock biomass $B(t)$, Equation (16), when $0 < n < 1$. Should $\dot{Y} > \dot{P}$, biomass declines from initial value B_0 towards adjustment level B_*. But when $\dot{Y} < \dot{P}$, biomass increases from B_0 towards B_*.

trary B_0, that $\dot{Y} < \dot{P}$ in Equation (15), mortality F must have a value such that

$$0 \leq F < \frac{\gamma m}{B_\infty}\left[1 - \frac{B_0{}^{n-1}}{B_\infty{}^{n-1}}\right],$$

in which case $\dot{B} > 0$ and the positive branch of Equation (15) applies. Trajectory $B(t)$ then increases, in accord with Equation (16), from initial value B_0 towards a higher adjustment level B_*. But for any value of F such that

$$F > \frac{\gamma m}{B_\infty}\left[1 - \frac{B_0{}^{n-1}}{B_\infty{}^{n-1}}\right],$$

then $\dot{Y} > \dot{P}$ and the negative branch of Equation (15) applies; trajectory $B(t)$ decreases from B_0 towards a lower adjustment level B_*.

Although the sign of $\dot{B}$ and the consequential course of $B(t)$ is a density-dependent process for given F, we should note here that when

$$F = \left[\frac{n-1}{n}\right] \frac{\gamma m}{B_\infty}, \qquad (17)$$

then $B(t) \rightarrow \dot{Y}$ and $\rightarrow m$, irrespective of initial conditions. Accordingly, we may identify parameter m with MSY in any of the (reformulated) rate equations of the system.

As indicated by Figures 7 and 8, the biomass level p where m occurs must lie on the range $B_\infty/e < p < B_\infty$ when $n > 1$. And with n so prescribed, root B_* of Equation (15) may have positive or negative values accordingly as F has a value less or greater than the critical ratio $\gamma m/B_\infty$. Figure 7 illustrates the behavior of Equations (15) and (16) for the constraints

$$n > 1$$
$$0 \leq F < \frac{\gamma m}{B_\infty}$$
$$0 < B_* \leq B_\infty,$$

in which case, root B_* of Equation (15) becomes the adjustment level such that $B(t) \rightarrow B_*$ by Equation (16). But whether $B(t)$ trends up or down to B_* depends on the further partitioning of F with respect to initial biomass value B_0. To insure, for arbitrary B_0, that $\dot{Y} < \dot{P}$ in Equation (15), mortality F must be further constrained to the interval

$$0 \leq F < \frac{\gamma m}{B_\infty}\left[1 - \frac{B_0{}^{n-1}}{B_\infty{}^{n-1}}\right];$$

thus $\dot{B} > 0$ and the positive branch of Equation (15) applies as indicated by Figure 7a. Trajectory $B(t)$ then increases, in accord with Equation (16), from initial value B_0 towards a higher adjustment level B_*, as indicated by the lower curve of Figure 7b. But for any value of F on the interval

$$\frac{\gamma m}{B_\infty}\left[1 - \frac{B_0{}^{n-1}}{B_\infty{}^{n-1}}\right] < F < \frac{\gamma m}{B_\infty},$$

then $\dot{Y} > \dot{P}$, $\dot{B} < 0$, and the negative branch of Equation (15) applies; trajectory $B(t)$ decreases from B_0 towards a lower adjustment level B_* as indicated by the upper curve of Figure 7b.

Should mortality F equal or exceed the critical ratio $\gamma m/B_\infty$ in a Pella-Tomlinson system where n exceeds unity, the corresponding stock, over sufficient time, will trend to extinction. Figure 8 illustrates the behavior of Equations (15) and (16) for the constraints

$$n > 1$$
$$F \geq \frac{\gamma m}{B_\infty}$$
$$B_* \leq 0,$$

in which case the zero root of Equation (15) applies, and we have $\dot{B} < 0$ and $B(t) \rightarrow 0$, irrespective of initial conditions.

By expanding the asymptotic bound of Equation (16) to a region of radius $\epsilon \cdot B_*$, and by appealing to arguments similar to those that led to the delay estimate (Equation (8)) of the Graham system, we calculate from Equation (16) the transition times for a Pella-Tomlinson stock as being

$$t_{\text{lag}} = \frac{B_\infty}{(1-n)(\gamma m - F_1 B_\infty)} \ln\left[\frac{1 - (1 \pm \epsilon)^{1-n}}{1 - (B_0/B_1)^{1-n}}\right] \qquad (18)$$

where ϵ represents the imprecision of stock-abundance estimates, and where B_0 and B_1 signify initial and adjustment levels as they correspond to mortality values F_0 and F_1. Again we suppose that F changes abruptly at zero reference time from value F_0 to the new value F_1, the plus sign of Equation (18) applying when $F_1 > F_0$ and the minus sign when $F_1 < F_0$.

By Equation (4) and the assumption that F varies in time by taking on fixed values of finite duration, we can write the transient yield rate for the Pella-Tomlinson system in the consolidated form

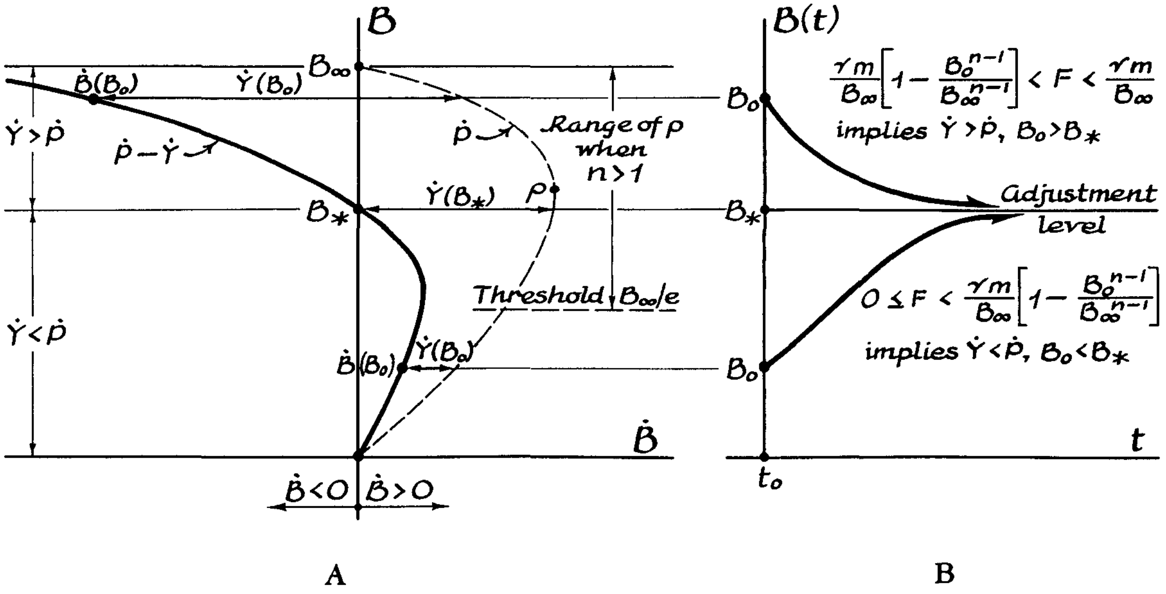


FIGURE 7.—A. Typical phase-plane graph of Equation (15) when $n>1$ and $F<\gamma m/B_\infty$, in which case root $B_*>0$. Should $\dot{Y}>\dot{P}$, the negative branch of Equation (15) applies; should $\dot{Y}<\dot{P}$, the positive branch applies. B. Typical solution trajectories, Equation (16), when $n>1$ and $F<\gamma m/B_\infty$. Should $\dot{Y}>\dot{P}$, biomass trajectory $B(t)$ declines from initial value B_0 toward adjustment level B_*. Should $\dot{Y}<\dot{P}$, $B(t)$ increases from B_0 toward B_*.

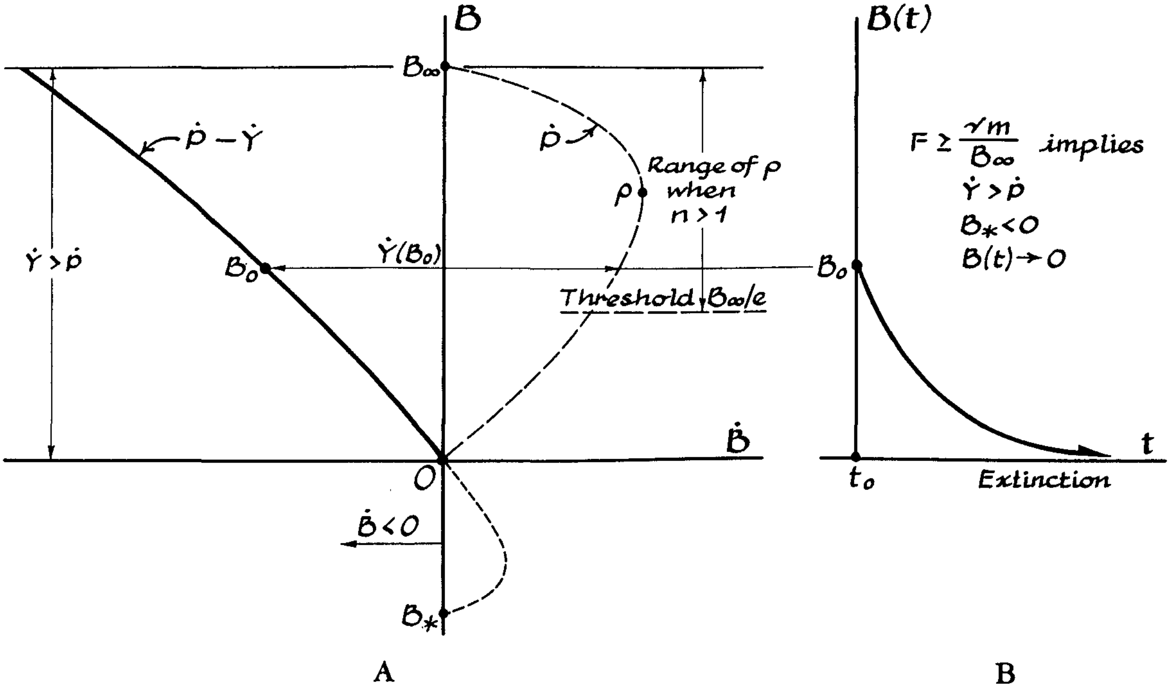


FIGURE 8.—A. Phase-plane graph of net productivity Equation (15) when $n>1$ and $F \geqslant \gamma m/B_\infty$. For any such combination of n and F, $B_* < 0$ and the zero root of Equation (15) applies. B. Typical solution trajectory, Equation (16), when $n>1$ and $F \geqslant \gamma m/B_\infty$, in which case the stock declines from initial value B_0 towards extinction.

$$\dot{Y}(t) = FB_* \left[1 - \left(1 - (B_0/B_*)^{1-n}\right) \exp\left((\gamma m/B_\infty - F)(1-n)\, t\right)\right]^{1/(1-n)} \qquad (19)$$

which is valid for all values of n save $n = 1$. Owing to the range of definition on exponent $1/1-n$, I have not found a closed form for the general time integral of Equation (19) (although existence is fairly easy to show for n positive and either less or greater than unity). But the usefulness of the analysis does not suffer too greatly for that omission, since one may accommodate Equation (19) to a numerical equation solver for finite measures of yield δY on associated intervals δt.

When F changes abruptly (as we have assumed throughout), yield rate $\dot{Y}$ changes abruptly, but the ensuing trends of adjustment are governed, in the Pella-Tomlinson system, by the following relationships:

$0 < n < 1$:
$0 < F < \infty$; stock size $B(t) \rightarrow B_*$ (Figure 6), which implies that $\dot{Y} \rightarrow FB_*$.
$n > 1$:
$F < \gamma m/B_\infty$; stock size $B(t) \rightarrow B_*$ (Figure 7), which implies that $\dot{Y} \rightarrow FB_*$.
$F \geqslant \gamma m/B_\infty$; stock size $B(t) \rightarrow 0$ (Figure 8), which implies that $\dot{Y} \rightarrow 0$.
$n > 0$ (both ranges):
$F = (1-1/n)\gamma m/B_\infty$; stock size $B(t) \rightarrow p$, which implies that $\dot{Y} \rightarrow m$ (and we may identify maximum latent productivity m with maximum yield rate in any of the time-dependent formulations of the analysis).

The quantity $\gamma m/B_\infty$, which plays such a prominent role in the analysis, can be identified as the "intrinsic growth rate" of the stock whenever exponent $n > 1$, in direct analogy to quantity k of the Graham system (and, in fact, with $n = 2$, then $\gamma = 4$ and $4m/B_\infty \equiv k$). But as a consequence of the indeterminate power form of the Pella-Tomlinson system and the switching of coefficient signs in the governing equations, the intrinsic growth rate turns out to be density-dependent when n takes on values between zero and unity. That is, by Equation (12), the intrinsic rate (if we may call it so) has the form

$$-\frac{\gamma m}{B_\infty} B^{n-1}$$

when n falls on the interval $0 < n < 1$ (in which case, $\gamma < 0$).

DISCUSSION

Any nonlinear stock-production system may be restructured along the lines of the critical-point analysis described in the foregoing sections; such a treatment will generate parametric variables most likely to be those essential to management analysis. A synopsis of the parameters that appear in the restructured Graham and Pella-Tomlinson systems is given by Table 1.

TABLE 1.—Parameters of the restructured Graham and Pella-Tomlinson systems as they apply to management components.

	Control parameters	
Management components	Graham system	Pella-Tomlinson system
Maximum stock size	B_∞	B_∞
Maximum productivity (corresponds to MSY)	m	m
Stock size for maximum productivity (the "optimum" stock size)	$B_\infty/2$ (fixed)	p
Ratio p/B_∞	½(fixed)	$n^{1/(1-n)}$
Fishing mortality	F	F
General adjustment level (consult text for mortality conditions)	B_*, or 0	B_*, or 0
Fishing mortality for adjustment level p (the "optimum" F)	$2\ m/B_\infty$	$(1 - 1/n)\ \gamma m/B_\infty$
Graph curvature	fixed	n

For optimization procedures on the Graham system, the essential parameters are $\{F, m, B_\infty\}$ augmented by the auxiliary parameters B_0 and B_*. For the Pella-Tomlinson system we may choose the combination $\{F, m, p, B_\infty\}$ or the combination $\{F, m, n, B_\infty\}$, either of which constitutes an essential set of mutually independent parameters. In the first set, p and B_∞ determine n; in the second, n and B_∞ determine p. The relationships in either case are governed by Equation (14).

Although the parametric influence of n is wholly prescribed by the ratio p/B_∞, exponent n also determines the curvature of all graphs of the Pella-Tomlinson system. Therefore, when the particularization of the system depends primarily on general curve fitting, the likelihood always exists that ill-determination of parameters will follow, owing to stochastic displacement of datum points at biomass levels remote from locations p and B_∞. As revealed by Equation (14), exponent n is quite unstable to small perturbations in the ratio p/B_∞. The variational response in n exceeds the perturbation in p/B_∞ by an order of magnitude near $n = 1$, and the instability increases as $p/B_\infty \rightarrow 1$. But the location of p with respect to B_∞ is far more critical to management analysis than graph curvature and its associated "good fit," since, to the left of p, the stock produces biomass at a positively accelerated rate, while to the right of p productivity decelerates.

The trait of degeneracy in the system has been noted by Pella and Tomlinson (1969) and by Fox (1971, 1975), but the exact relationships between exponent n and the quantities m, p, and B_∞ have been obscured heretofore by the conventional castings of the system. With the restructured governing equations and the explicit formulations of critical parameters, much of the statistical degeneracy associated with previous routines can be constrained. And since the management parameters appear directly in the equations of the system, their variances can be calculated directly in the estimation procedure and appeals to indirect methods are avoided.

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