DEPARTMENT OF MATHEMATICS

OPTIMAL GROWTH STRATEGIES WHEN MORTALITY AND PRODUCTION RATES ARE SIZE–DEPENDENT

by

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Numerical Analysis Report 12/92

UNIVERSITY OF READING

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Abstract

Pontryagin's maximum principle from optimal control theory is used to find the optimal allocation of energy between growth and reproduction when lifespan may be finite and the trade-off between growth and reproduction is linear. Analyses of the optimal allocation problem to date have generally yielded 'bang-bang' solutions, i.e. determinate growth: life-histories in which growth is followed by reproduction, with no intermediate phase of simultaneous reproduction and growth. Here we show that an intermediate strategy (indeterminate growth) can be selected for if the rates of production and mortality either both increase, or both decrease with increasing body size; this arises as a singular solution to the problem. Our conclusion is that indeterminate growth is optimal in more cases than had been realised. The relevance of our results to natural situations is discussed.

Introduction

Two main patterns have been recognized with respect to the way organisms allocate energy between growth and reproduction (Sibly, Calow & Nichols, 1985). We shall say organisms have *determinate growth* if they stop growth when they become mature. This is what engineers would call a bang-bang strategy. Alternatively if the organisms continue growing while reproducing they are said to have *indeterminate growth*. This usage is quite common (e.g. Sibly *et al*, 1985; Kozlowski & Wiegert, 1987), but the terms have also been used with different meanings (e.g. Sebens, 1987).

Under which circumstances should each of these two patterns be selected for? Most situations analysed to date have had determinate growth as an optimal strategy. This is surprising given the ubiquity of indeterminate growth in nature. Previous analyses of this problem include Taylor *et al*, (1974) and Sibly *et al*, (1985), who used models of the same type as ours described below, but restricted to infinite lifespan. By lifespan we here mean maximum reproductive age. Ziolko & Kozlowski (1983) explicitly investigated the effect of lifespan on optimal life history, but they did not allow size-dependent mortality. All these analyses yielded bang-bang solutions (except in some of the cases of non-linear trade-offs analysed by Sibly *et al*, (1985)). However, Gabriel (1982) using numerical methods showed that indeterminate growth could be optimal if lifespan was finite and both production and mortality rates increased with size.

Here we develop a generalized analytical model which includes the previous treatments as special cases, and treats the case considered by Gabriel (1982) analytically.

The Optimal Control Problem

Following earlier treatments (Leon (1976), Alexander (1982), Sibly et al, (1985)) we consider the allocation process as a problem in optimal control theory, in which a performance criterion, here fitness, is maximised by the choice of a control variable (allocation of resources between growth and reproduction). First we give precise meaning to these terms.

Fitness maximization

We follow Charlesworth (1980) and most modern treatments in supposing that the fitness of a life-cycle strategy is best measured by its per capita rate of increase, r, defined by the equation

$$1 = \int_0^T e^{-rt}\, l(t)\, b(t)\, dt \qquad (1)$$

where t is age, l(t) is survivorship from birth until age t, b(t) is the rate of giving birth, and T is maximum reproductive age.

In common with most life-cycle theorists we search for strategies which maximise fitness since those strategies are likely final products of evolution.

Model of Growth and Reproduction

Of the total energy, $P(W)$, available to an organism of a given size, W, for production, at some stage some must be used for reproduction. There is, in a sense, always competition between somatic growth and reproduction for a share of $P(W)$, and here we consider how that should be resolved. We shall not consider here the problems of optimising $P(W)$, instead we shall assume it is given, as a function of W. Our notation is

t = age.

$W(t)$ = body mass; $W(0)$ = initial body mass.

$P(W)$ = production = total power devoted to growth and reproduction, given in this analysis; $P \geq 0$. We assume the units of energy are such that allocation of one unit of power to growth results in unit growth rate.

W_o = energy cost of producing one offspring; $W_o = W(0)/k$ where k represents the efficiency of offspring production.

$u(t)$ = fraction of P devoted to reproduction; $0 \leq u \leq 1$. Production not used for reproduction is assumed to be used exclusively for growth.

$b(u,W)$ = rate at which adults of size W give birth $= u(t)\, P(W)/W_o$.

$\mu(W)$ = mortality rate, assumed to be uniquely determined by W.

$l(t)$ = survivorship from birth to age t,

$$i.e. \quad l(t) = e^{-\int_0^t \mu(x)\,dx}.$$

From this we define a new variable:

$$L(t) = e^{-rt}\, l(t);\ L(0) = 1. \tag{2}$$

The justification for linking e^{-rt} and l(t) into a single 'state' variable lies in the fact that taking account of the rate of increase of the population is mathematically equivalent to adding a constant term r to the mortality rate. L(t) is a factor weighting fecundity in equation (1), and decreases with time at rate $r + \mu(W)$. Fecundity loses value with time partly because the population is increasing at rate r and partly because survival probability decreases at rate $\mu(W)$.

These variables are necessarily related by

$$\dot{W} = (1-u(t))\,P(W) \tag{3}$$

and

$$\dot{L} = -\,m(W)\ L(t) \tag{4}$$

where

$$m(W) = r + \mu(W) \tag{5}$$

and the dot $(\cdot)$ denotes differentiation with respect to time.

Equation (1) can now be rewritten

$$\int_0^T \frac{uP(W)}{W_0} L\,dt = 1. \tag{6}$$

The optimal control problem is to choose u to maximize r subject to equations (3), (4) and (6), and the constraint $0 \le u \le 1$.

Optimization Technique

Although our results can be obtained using the technique of Taylor et al (1974), we prefer to maximise r directly. We use Pontryagin's Maximum Principle (PMP) (Bryson & Ho, 1969; Intriligator, 1971; Clark, 1976; Banks, 1986) to solve the 'Mayer' problem of choosing a vector 'control' variable $\underline{u}(t)$ for all values of t from initial time 0 to terminal time T so as to maximize the function

$$J(\underline{u}) = F(\underline{x}(T)) \tag{7}$$

subject to

$$\dot{\underline{x}} = \underline{g}[\underline{x}(t), \underline{u}(t)], \tag{8}$$

where $\underline{x}(0)$ and T are fixed. Symbols underlined represent vector variables. Equation (8) is referred to as the 'state equation' and relates $\underline{x}$, referred to as the state variable, to control variable $\underline{u}(t)$. One of the conditions that must be satisfied by the solution is that for every value of t from 0 to T, $\underline{u}(t)$ must have the value that maximizes the 'Hamiltonian':

$$H = \underline{\lambda}(t) \cdot \underline{g}[\underline{x}(t), \underline{u}(t)] \tag{9}$$

in which $\underline{\lambda}(t)$ is a continuous function of t such that

$$\dot{\underline{\lambda}} = -\frac{\partial H}{\partial \underline{x}} \tag{10}$$

and, if $x_i(T)$ is unconstrained,

$$\lambda_i(T) = \frac{\partial F}{\partial x_i}\Big|_{x(T)}, \tag{11}$$

but if $x_i(T)$ is fixed, then $\lambda_i(T)$ is free . This is an example of a split-boundary condition problem.

The Optimal Strategy

$$\text{Let } \phi(t) = \int_0^t \frac{uLP(W)}{W_0} d\tau ; \tag{12}$$

$\phi(0)=0$ and $\phi(T)=1$ from equation (6).

In our problem J=r and ϕ, W, L and r are the state variables. The derivatives of the state variables (equation (8)) are $\dot{\phi}, \dot{W}, \dot{L}$ and $\dot{r}$. From equation (12),

$$\dot{\phi} = \frac{uLP(W)}{W_0}, \tag{13}$$

and $\dot{W}$ and $\dot{L}$ are given by equations (3) and (4). Since r is not a function of age $\dot{r} = 0$.

Equation (9) now gives a necessary condition for an allocation strategy u(t) to maximize r:-

$$\max_{u(t)} H(t) = \lambda_0 u(t) \frac{L(t)\ P(W)}{W_0} + \lambda_1(t)(1-u(t))P(W) - \lambda_2(t)m(W)L(t). \tag{14}$$

where λ_0, λ_1, λ_2 and λ_3 are the 'costate' variables associated with $\dot{\phi}, \dot{W}, \dot{L}$ and $\dot{r}$ respectively. λ_3 does not appear in (14) because $\dot{r} = 0$.

From (10) $\dot{\lambda}_0 = 0$, so λ_0 is a constant. As shown in Appendix 1,

$$\lambda_0 = \lambda_2(0), \text{ which we write } \gamma. \tag{15}$$

$\lambda_1(t)$ and $\lambda_2(t)$ are functions to be determined later; from (10) they are specified by:

$$\dot{\lambda}_1 = \lambda_2 m' L - [u\frac{\gamma L}{W_o} + (1-u)\lambda_1]\ P' \tag{16}$$

where dash (') denotes differentiation with respect to W,

$$\dot{\lambda}_2 = \lambda_2 m(W) - u\frac{\gamma P(W)}{W_o} \tag{17}$$

and, from (11)

$$\lambda_1(T) = \lambda_2(T) = 0. \tag{18}$$

Because the trade-off between fecundity and growth is linear and mortality is independent of the control variable u, it follows that the Hamiltonian (equation 14) is linear in u, and its derivative, the so-called switching function (Bryson & Ho, 1969; Intriligator, 1971) is not explicitly dependent on u:

$$\frac{\partial H}{\partial u} = P(W)\,(\frac{\gamma L}{W_o} - \lambda_1) \tag{19}$$

To maximize H, therefore, the optimal control, written u^*, must be either 0 or 1, according to the relative values of $\gamma L/W_o$ and λ_1:

$$u^* = 0 \text{ when } \gamma L/W_o < \lambda_1, \tag{20}$$

and

$$u^* = 1 \text{ when } \gamma L/W_o > \lambda_1. \tag{21}$$

In other words, a boundary solution always maximizes the Hamiltonian.

Since offspring are necessarily smaller than adults, all resources must be allocated to growth in the initial part of the life cycle, and at T, if not before, all resources should be allocated to reproduction since investment in growth would then be wasted, because adults do not reproduce after age T. It is clear therefore that initally $\gamma L/W_o < \lambda_1$, with optimal strategy $u^* = 0$ (from 20), and finally $\gamma L/W_o > \lambda_1$, with optimal strategy $u^* = 1$ (from 21), so that all resources are allocated to reproduction and size is constant until death. Since $\lambda_1 > \gamma L/W_o$ initially but finally $\lambda_1 < \gamma L/W_o$, it follows that λ_1 changes more rapidly than $\gamma L/W_o$, and therefore at some time before T the two functions must cross. We deal later with the case that during the crossover the two functions are equal over some nonzero period of time (when they follow a 'singular arc'). Assume for the moment that that does not occur, and the functions cross cleanly: if they only cross once the optimal strategy is a simple two-phase strategy: growth followed by reproduction. Although we have not established that there are not more than two bang-bang phases (e.g. growth-reproduction-growth-reproduction), these do not occur in biological examples in non-seasonal environments, so far as we know, and we shall not consider them further here.

The two-phase optimal control problem

Now suppose, for the moment, that the solution is bang-bang, in two phases, as described above, devoting all resources to growth in the first phase, and all to reproduction in the second. The point at which the initial phase ends will be referred to as the first switching point and denoted by subscript 1; thus switching time is t_1, and bodymass is then W_1. Similarly the start of the final phase will be referred to as the second switching point, t_2, with associated bodymass W_2. Of course, in the two phase problem these two points coincide ($t_1=t_2$, $W_1=W_2$), but by keeping them distinct we are able to derive relationships with wider generality which we use later in analysing singular arcs.

The two-phase optimal control problem can now be stated formally as follows. For given T and W_0, find the bang-bang strategy characterised by W_2, and associated t_2 and r, which maximises r in (1).

To find the solution, note that in the first phase all resources are allocated to growth, so $\frac{dW}{dt}=P(W)$ from (3),

and hence

$$t_1=\int_{kW_0}^{W_1}\frac{dW}{P(W)}\,. \tag{22}$$

From (4) and L(0) = 1,

$$L(t)=e^{-\int_0^t (r+\mu(W))\,dt}=e^{-\int_{kW_0}^{W(t)}\frac{r+\mu(W)}{P(W)}\,dW}$$

during the first phase, so that

$$L_1 = e^{-\int_{kW_0}^{W_1} \frac{r+\mu(W)}{P(W)} dW} . \tag{23}$$

During the final phase $W(t) = W_2$ and from (4), $L(t) = e^{-(r+\mu_2)(t-t_2)} L_2$. Hence from (6),

$$1 = \int_{t_2}^{T} \frac{P_2 L(t)}{W_0} dt = \frac{P_2 L_2}{W_0} \int_{t_2}^{T} e^{-(r+\mu_2)(t-t_2)} dt = \frac{P_2 L_2}{W_0 (r+\mu_2)} (1 - e^{-(r+\mu_2)(T-t_2)}) \tag{24}$$

where $W_2 = W_1$, $P_2 = P(W_2)$, $\mu_2 = \mu(W_2)$, $L_2 = L_1$ is given by (23) and $t_2 = t_1$ by (22).

For given T and W_0 and relationships P(W) and $\mu(W)$, it can be seen that since P_2, L_2, μ_2 and t_2 are determined by W_2, (24) provides a relationship between r and W_2 of the form $f(W_2, r) = 1$. The relationship between r and W_2 can readily be graphed and the optimal strategy, i.e. that value of W_2 which maximises r, can be found by inspection (example in Fig. 1). The optimal control problem is therefore reduced to a simple static problem of the form: given $f(W_2, r) = 1$, find W_2 that maximises r.

A necessary condition for optimality is that $\frac{dr}{dW_2} = -\frac{\partial f}{\partial W_2} / \frac{\partial f}{\partial r} = 0$, or $\frac{\partial f}{\partial W_2} = 0$ (assuming $\frac{\partial f}{\partial r} \neq 0$). This equation can obtained from (24) as

$$m_2'\frac{P_2}{m_2}(T-t_2)e^{-m_2(T-t_2)} + \left(\frac{P_2}{m_2}\right)'(1 - e^{-m_2(T-t_2)}) - 1 = 0 \qquad (25)$$

where $m_2 = r + \mu_2$, and $m_2' = \mu_2'$ and $t_2 = t_2(W_2) \equiv t_1(W_1)$ is determined by (22). Differentiation denoted by ' is here thought of as with respect to W_2.

Size at the second switching point, W_2, must therefore satisfy equation (25), which specifies a relationship between r and W_2 for fixed T. However r and W_2 must also satisfy (24), and hence r can in principle be eliminated between (24) and (25) to obtain the optimal W_2, as shown graphically in Fig. 1. This completes the solution of the two-phase optimal control problem.

Singular arcs

In the two-phase optimal control problem we assumed that when λ_1 meets $\gamma L/W_0$ the two functions cross cleanly, but if not then $\lambda_1=\gamma L/W_0$ over some finite time interval. The history of optimal control shows that ignoring this possibility can lead to error. Accordingly we here explore the implications of intermediate control, giving rise to $\lambda_1=\gamma L/W_0$, being an optimal strategy over a non-zero period of time. During this period u must be such that $\frac{\partial H}{\partial u} = 0$. The trajectory during such a period is known as a singular arc (e.g. Bell & Jacobson, 1975).

Since biological considerations show that the optimal trajectory is initially all growth and finally all reproduction, the only possible position for a singular arc is in the middle of the life history. During the singular arc

$$\lambda_1=\gamma L/W_0, \tag{26}$$

and this holds during a non-zero period of time which we shall call the singular period. Hence

$$\dot{\lambda}_1 = \gamma \dot{L}/W_o \tag{27}$$

Substituting (4) and (16) into (27), and using (26), gives:

$$\lambda_2 = \frac{\gamma(P'-m(W))}{W_0 m'} \tag{28}$$

throughout the singular period, where as before ' denotes differentiation with respect to W.

Three phase strategy

For a three-phase optimal strategy, containing a singular arc, the initial phase is characterized by the same equations (22) and (23) as in the two-phase strategy. Similarly during the terminal period, u = 1 and W = W_2, so λ_2 can be found from (17) and (18) as

$$\lambda_2 = (1-e^{-m_2(T-t)})\frac{\gamma P_2}{W_0 m_2} \tag{29}$$

Substituting (29) into (16) and integrating within the terminal period from t to T (noting that from (4) $L(t) = L(T)e^{m_2(T-t)}$) gives:

$$\frac{\lambda_1 W_0}{\gamma} = m_2{}' \frac{P_2}{m_2} L(T)(T-t) + (\frac{P_2}{m_2})'[L(t)-L(T)] \tag{30}$$

At the start of the terminal period $\lambda_1 W_0/\gamma = L(T)e^{m_2(T-t_2)}$, and substituting this into (30) gives equation (25) again. This shows that the switching point t_2 initiating the terminal period satisfies equation (25) even if the optimal strategy is not bang bang. Of course if the optimal strategy is not bang bang, the switching time t_2 is no longer tied to switching size W_2 by equation (22), so equation (25) now acts as a constraint on the three variables W_2, r and t_2 restricting them to a surface in W_2-r-t_2 space (Fig. 2). Because it specifies a criterion satisfied by the optimal solution, we will refer to (25) in general as the criterion equation. Note however that in the three-phase strategy two more equations in W_2, r and t_2 are needed to specify the optimal switching point uniquely.

Joining the Singular Period to the Terminal Period

Equations (29) and (28) describe the trajectories of λ_2 during the terminal and singular periods respectively: the two trajectories meet at the 'second switching point' when t = t_2 and the following must hold:

$$(T-t_2)m_2 = -\ln[1-\frac{m_2}{P_2}\frac{P_2{}'-m_2}{m_2{}'}] \tag{31}$$

Equation (31) gives the value of t_2 at the end of the singular period, which is the moment when the terminal period starts, i.e. the final switching point. This is the second of the three equations in W_2, r and t_2 needed to find the parameters of the optimal final switching point.

Since the final switching point satisfies the criterion equation, we can substitute $T-t_2$ from (31) into (25) to obtain:

$$\frac{m_2}{P_2}\,\frac{P_2'}{m_2'} = -\ln\left[1 - \frac{m_2}{P_2}\,\frac{P_2'-m_2}{m_2'}\right]. \tag{32}$$

Using (32), equation (31) may be rewritten as:

$$T-t_2 = \frac{1}{P_2}\,\frac{P_2'}{m_2'}. \tag{33}$$

For fixed r = r*, the optimal value of r, the criterion equation (25) specifies a relationship between W_2 and t_2, which we shall refer to as the switching curve (Figs. 2 and 3), for reasons that will become apparent (see Fig. 4). It is worth noting that equation (33) characterizes a stationary point of W_2 as a function of t_2, implicitly defined by this switching curve: taking the partial derivative of (25) relative to t_2, with fixed r, while setting $dW_2/dt_2 = 0$, gives (33).

Necessary Conditions for a Singular Arc

The preceding sections show that for a singular arc to exist equations (32) and (33) must hold. Whether this is possible depends on the actual shapes of the size-specific production and mortality functions. We now obtain necessary conditions for (32) and (33) to hold. From (33) P_2' and m_2' must have the same sign for $T-t_2$ to be positive. Thus mortality and production must either both increase with size or both decrease with size for equation (32) to have a solution. Let us assume first that these rates increase with size. It can be shown (Appendix 2) that m(W) is necessarily positive at the switching point if $\mu(W)$ increases with size; this result also allows us to disregard the case $m_2 = 0$, which would otherwise be a candidate solution to (32). The left-hand side of (32), therefore, is positive, so that the term in brackets in the right-hand side must be smaller than one; this is only possible if $P_2' > m_2$. Furthermore, $(\frac{P_2}{m_2})'$ must also be smaller than 1, otherwise this term in brackets becomes negative.

Thus, assuming $P_2' > 0$, necessary conditions for the existence of a stationary point of the criterion curve and ipso facto of a singular arc, are that, at the stationary point:

$$m_2' > 0, \tag{34}$$

$$P_2' > m_2, \tag{35}$$

$$(\frac{P_2}{m_2})' < 1. \tag{36}$$

A further condition for local optimality, which holds throughout the singular arc, is given by the second order Clebsch-Legendre condition (Bell & Jacobson, 1975; see Appendix 3):

$$(\frac{P'-m}{m'})' < 1. \tag{37}$$

Let us assume now that production rate is a decreasing function of body size. This is a quite plausible assumption, at least over some size range: growth curves are often sigmoid, implying that production rate first increases, then decreases with body size. Thus, production rate often decreases with body size on the upper part of the size range, which is the part of interest because maturity occurs there. An analysis similar to that provided here shows that in this case ($P_2'<0$), the necessary conditions for a singular arc are that, at the stationary point:

$$m_2' < 0, \tag{38}$$

$$\left(\frac{P_2}{m_2}\right)' > 1, \tag{39}$$

and the Clebsch-Legendre condition $\left(\frac{P_2'-m_2}{m_2'}\right)' > 1.$ (40)

A specific example is developed below where production and mortality rates both increase with size. This example shows that conditions (34) - (37) can be satisfied, and equation (32) can have a solution. Before presenting the numerical example, we derive the optimal control during the singular period, for the general case. Then we join the initial period to the singular period, in order to provide a complete solution over the whole life cycle.

Optimal Control During the Singular Period

The two terms in equation (28) must be equal during the whole singular period, so that:

$$\dot{\lambda}_2 = \frac{\gamma}{W_o} \frac{d}{dt} \left[\frac{P'-m}{m'}\right] \tag{41}$$

Using (3) and (17) in (41):

$$\lambda_2 m(W) \frac{W_0}{\gamma} - uP(W) = \left(\frac{P'-m}{m'}\right)' (1-u) P(W), \tag{42}$$

and using (28) the optimal control u* is defined during the singular period by:

$$u^* \left(\left(\frac{P'-m}{m'}\right)'-1\right) = \left(\frac{P'-m}{m'}\right)' - \frac{m}{P} \frac{P'-m}{m'} \tag{43}$$

Substituting into equation (3) gives:

$$\dot{W} = \frac{\left(\frac{P'-m}{m'}\right) m - P}{\left(\frac{P'-m}{m'}\right)' - 1}, = G(W,r), \text{ say} \tag{44}$$

Hence $\int_{t_1}^{t_2} dt = \int_{W_1}^{W_2} \frac{dW}{G(W,r)}$ giving $t_2 - t_1 = \int_{W_1}^{W_2} \frac{dW}{G(W,r)}$. (45)

Similarly (44) can be used with (4) and (23) to find L during the singular arc:-

$$L(t) = e^{-\int_{kW_0}^{W_1} \frac{r+\mu(W)}{P(W)} dW - \int_{W_1}^{W} \frac{r+\mu(W)}{G(W,r)} dW} \tag{46}$$

Using this in (6) and using uP = P - G during the singular arc (from (3) and (44)), we obtain the singular-arc analogue of (24):-

$$1 = \int_{W_1}^{W_2} \frac{(P(W)-G(W,r))\, e^{-\int_{kW_0}^{W_1} \frac{r+\mu(W)}{P(W)} dW - \int_{W_1}^{W} \frac{r+\mu(W)}{G(W,r)} dW}}{W_0 G(W,r)} dW +$$

$$\frac{P_2 e^{-\int_{kW_0}^{W_1} \frac{r+\mu(W)}{P(W)} dW - \int_{W_1}^{W_2} \frac{r+\mu(W)}{G(W,r)} dW}}{W_0(r+\mu_2)} (1-e^{-(r+\mu_2)(T-t_2)}) \qquad (47)$$

Equations (22) and (33) define t_1, t_2 as functions of W_1, W_2 respectively. Then (25) (45) and (47) give 3 equations with which to find W_1, W_2 and r.

A Numerical Example

For the purpose of illustration, a numerical example will now be given, which is directly relevant to Gabriel's (1982) numerical simulations. Following Gabriel (1982), production and mortality rates will be taken increasing with size; more specifically we will assume both rates proportional to size, so that $P(W) = cW$ and $\mu(W) = Wd$, for some positive constants c and d. We assume that k is such that r = 0 for the optimal strategy. Although some features of the example may be unrealistic, it has the virtue of analytic simplicity.

For the case that r=0 the switching curve (obtained from equation (25) with r=0, see p.16 and Fig. 2) reduces to:

$$W_2 = \frac{\ln[c(T-t_2)]}{(T-t_2)d} \tag{48}$$

This is shown in Fig. 3, with c and d set to 0.0702 and 0.01, respectively. From equation (33), the end of the singular period is:

$$W_2 = c/ed \tag{49}$$

and

$$t_2 = T-e/c \tag{50}$$

where e is the base of natural logarithms. As expected, this point coincides with the stationary point of the switching curve (Fig. 3). Using (43) and (44), the optimal control u* during this singular period, is given by:

$$u^* = 1-(Wd/2c) \tag{51}$$

It is worth noting that, in this particular case, the optimal reproductive effort u* decreases with size, and therefore with age, during the singular period. Using (3), size during this singular period (the singular arc) is:

$$W(t) = \frac{2c}{d(e+c(T-t))} \tag{52}$$

If size at birth is below the singular arc, then u*=0 during the initial period, when size is given by $W(t) = kW_oe^{ct}$. The optimal strategy (Fig. 3) is, therefore, to grow from birth exponentially until the singular arc (52) is reached, then to follow this arc, and finally to stop growing when the switching curve (48) is met at its stationary point (49,50).

Discussion

The main contribution of this paper is to extend existing analyses of growth and reproduction by considering the effects of size-dependent mortality and lifespan on the optimal strategy. The main results are shown in Fig. 4. In (a) the switching curve has no stationary point, i.e. is monotonic, so the optimal strategy is to grow until the weight-age trajectory meets the switching curve, then to switch to reproduction. In (b) the switching curve has a stationary point but the optimal strategy is again determinate growth. However if (and only if) the switching curve has a stationary point the optimal strategy may include, in the middle, a period when growth and reproduction should occur simultaneously (Fig. 4c). During this period the weight-age trajectory follows a singular arc satisfying equation (44). The optimal strategy in this case is to grow until the singular arc is reached, then to follow it, growing and reproducing simultaneously, until the singular arc terminates (at the stationary point of the switching curve), and then to devote all resources to reproduction.

FIG. 4

Note that the switching curves (dashed lines in Fig. 4) are only appropriate to the optimal growth trajectories shown. Other suboptimal growth strategies yield lower values of r and their switching points do not satisfy the criterion equation (25) from which the so-called switching curve is calculated (see Fig. 1).

It will be important to extend these analyses to consider the effect of lifespan on optimal strategy. Is it the case, for example, that indeterminate growth is only an optimal strategy for longer lifespans, other things being equal? This would appear likely intuitively, and fits our knowledge of animals and plants.

These results extend those of Taylor *et al*, (1974) and Sibly *et al* (1985) by introducing the possibility of a singular arc and by incorporating the effect of lifespan. When lifespan, T, tends to infinity, our results (equation (25)) reduce to those of Taylor *et al*, i.e. a switch from growth to reproduction should occur when

$$\frac{\partial}{\partial W}\left(\frac{P}{r^{*}+\mu}\right) = 1$$

(their equation (13)).

Equation (25) also generalizes some results of Ziolko & Kozlowski (1983) who showed that for constant mortality rate $\mu = \mu_0$ and fixed population size ($r = 0$) the optimal strategy is bang-bang, with a switch from growth to reproduction occurring when

$$\partial P/\partial W = \mu/(1-e^{-\mu(T-t)})$$

(their equation (31)). Our equation (25) reduces to their equation (31) under these same assumptions, and our analysis again introduces the possibility that intermediate strategies are optimal, this time by allowing size-dependent mortality, a common phenomenon in nature.

Our results also provide an analytical basis for Gabriel's (1982) numerical demonstration that intermediate strategies can be optimal if lifespan is finite and both production and mortality rates increase with size.

The main conclusion of the paper is that indeterminate growth can be an optimal strategy if production and mortality either both increase with size, or both decrease. This has the intuitive meaning that growth after reproduction entails simultaneous costs and benefits: growing further either increases production rate at the expense of survival, or improves survival at the expense of production; along the singular arc, the costs and benefits of growing further equalize over a non-zero period of time.

It is worth noting that King & Roughgarden (1982) also found a singular arc to be responsible for a gradual transition to reproduction in the case of annual organisms with an unpredictable season length. As a matter of fact, it should be noted, when applying these results to real organisms, that unpredictable season length (Cohen, 1971; King & Roughgarden, 1982; Amir & Cohen, 1990) as well as non-linear trade-offs (Sibly et al, 1985) can also lead to the optimal strategy being intermediate. No stochastic factors have been considered in our model, which is completely deterministic.

How relevant are these findings to real organisms, and how likely is it that conditions for a singular arc are met? In natural populations, mortality usually decreases with size (Ito, 1980). Furthermore, growth curves are frequently sigmoid (Sibly et al, 1985), implying that production rate first increases, then decreases with increasing body size. Thus, production rate often decreases with size over the range of interest, so that some of the necessary conditions (eq. 38-40) for a singular arc seem to be met quite often. This could be responsible for intermediate strategies in several instances. An empirical test of this idea could be performed by checking the size dependence of mortality and production rates in intermediate strategists, over the period of gradual transition to reproduction.

What about the reverse situation (eq. 34-37), with both rates of production and of mortality increasing with body size? Whereas, as pointed out above, mortality usually decreases with size in natural populations, the reverse is true under some special circumstances such as fish visual predation on planktonic crustaceans (Lynch, 1980; Gabriel, 1982). For the purpose of illustration, the patterns of growth in cladocerans is discussed hereafter.

From Lynch's (1980) review, it appears that the littoral species of cladocerans are bang-bang strategists, whereas the planktonic species are intermediate strategists. Without referring to a mathematical formalization, Lynch (1980) proposed an explanation for this trend based on patterns of size-dependent mortality. Littoral species are mainly under invertebrate predation at small sizes; the optimal strategy in this case would be to reach as fast as possible an adult size large enough to escape invertebrate predation, then to invest entirely in reproduction. In contrast, planktonic species are under both invertebrate predation at small sizes, and vertebrate predation at large sizes; the optimal strategy in this case would be to start reproducing at a small size, while fish predation is still relatively low, but meanwhile to continue growing, in order to reduce invertebrate predation.

Based on the conclusions of Sibly et al, (1985) (see introduction), Perrin et al, (1987) criticized this model, arguing that a size-dependent mortality could not induce an intermediate strategy. However, the results of the present analysis obviously oppose this latter argument; these results furthermore suggest an explanation to the above trend, slightly different from Lynch's, though also based on patterns of size-dependent mortality: bang-bang strategies are selected for in littoral species because mortality decreases as size increases, due to invertebrate predation at small sizes; by contrast, intermediate strategies are selected for in planktonic species because mortality increases with size, due to vertebrate predation at large sizes.

Since, furthermore, production rate appears to increase with body size in cladocerans, at least over the size range where maturity occurs (e.g. Gabriel, 1982; Taylor, 1985; Perrin et al, 1987), the general patterns of growth in this group, reviewed by Lynch (1980), seem to confirm the main prediction from the present model that a size dependent mortality might induce a gradual transition to reproduction.

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Appendix 1

Equations (6), (17), (4) and (2) imply

$$\gamma = \gamma\int_0^T \frac{uP(W)\,L}{W_0}\,dt = \int_0^T [(r+\mu)\lambda_2 L-\dot{\lambda}_2 L]\,dt + \int_0^T [(r+\mu)\lambda_2 L+\lambda_2 \dot{L}]\,dt-\lambda_2 L\Big|_0^T$$

$$= \int_0^T [(r+\mu)\lambda_2 L-(r+\mu)L\lambda_2]\,dt + \lambda_2(0)$$

Hence $\gamma = \lambda_2(0)$ (14)

Appendix 2

Let μ_α be the mortality rate of the largest animals, achieved during the terminal period. If $\mu(W)$ increases with size, the mean per capita mortality rate of the population, $\overline{\mu}$, is necessarily smaller than μ_∞:

$$\overline{\mu} < \mu_\infty \tag{A1}$$

The per capita rate of increase r* is the difference between the per capita rates of fecundity $\overline{\beta}$ and mortality $\overline{\mu}$:

$$r^* = \overline{\beta} - \overline{\mu} \tag{A2}$$

so that, from (A1) and (A2),

$$r^* + \mu_\infty > \overline{\beta} \tag{A3}$$

and, because fecundity cannot be negative, $m(W) = r^* + \mu(W)$ is necessarily positive during the whole terminal period, including the switching point.

Appendix 3

The Legendre-Clebsch second order condition for optimality of the singular control (Bell & Jacobson, 1975; Banks, 1986) is:

$$\frac{\partial}{\partial u}\left[\left(\frac{d}{dt}\right)^2\left(\frac{dH}{du}\right)\right] > 0 \qquad \text{(B1)}$$

From equation (19), the first time-derivative of dH/du is:

$$\frac{d}{dt}\left(\frac{dH}{du}\right) = \left(\frac{\gamma\,(P' - m)}{W_o} - \lambda_2 m'\right)PL \qquad \text{(B2)}$$

and the second time-derivative:

$$\left(\frac{d}{dt}\right)^2\left(\frac{dH}{du}\right) = \left(\frac{\gamma\,(P'-m)}{W_o} - \lambda_2 m'\right)\frac{d[PL]}{dt} + PL\left[(1-u)\,P\left(\frac{\gamma}{W_0}\,(P' - m)' - \lambda_2 m''\right) - m'\dot{\lambda}_2\right. \qquad \text{(B3)}$$

Using (17) and (28):

$$\frac{\partial}{\partial u}\left(\frac{d}{dt}\right)^2\left(\frac{dH}{du}\right) = \frac{P^2 L}{W_o}\left[m''\,\frac{P' - m}{m'} - (P' - m)' + m'\right] \qquad \text{(B4)}$$

From (B1), the term in brackets in the right-hand side must be positive, which is the case, assuming m' > 0, if:

$$\left(\frac{P' - m}{m'}\right)' < 1 \qquad \text{(B5)}$$

FIGURE CAPTIONS

Fig. 1. The solution of the two-phase optimal control problem can be found by plotting the relationship between r and W_2 (solid line) obtained from equation (24). Here k = 0.05, other parameters and relationships are as in Fig. 3. Also shown is the solution of the equation (25) (dashed line). Note that the optimal strategy (*) lies on the intersection of the two curves.

Fig. 2. The surface in W_2-r-t_2 space specified by the criterion equation (a) in 3-D, (b) as a contour map showing contours of W_2. Parameters as in Fig. 3. A slice through the surface at r = 0 gives the switching curve shown in Fig. 3. Note also that the solution of the criterion equation for the two-phase optimal control problem illustrated in Fig. 1 (dashed line in Fig. 1) corresponds to the intersection of this surface with the surface specified by equation (22).

Fig. 3. The growth curve W(t) (solid line), switching curve $W_2(t_2)$ (dashed line) and singular arc (dotted line) for the case analysed in the Numerical Example in which P = 0.0702W,
μ = 0.01W, T = 100, inital size = 0.25 and r = 0.

Fig. 4. The main types of growth curve (solid lines) and switching curve (dashed lines) considered in this paper. In (a) the switching curve is monotonic decreasing and the optimal strategy is determinate growth. In (b) the switching curve has a stationary point but the optimal strategy is again determinate growth. In (c) the switching curve has a stationary point and the optimal strategy is indeterminate growth, following a singular arc (dotted line) between the initial growth phase and the final reproductive phase. On the singular arc growth and reproduction occur simultaneously.

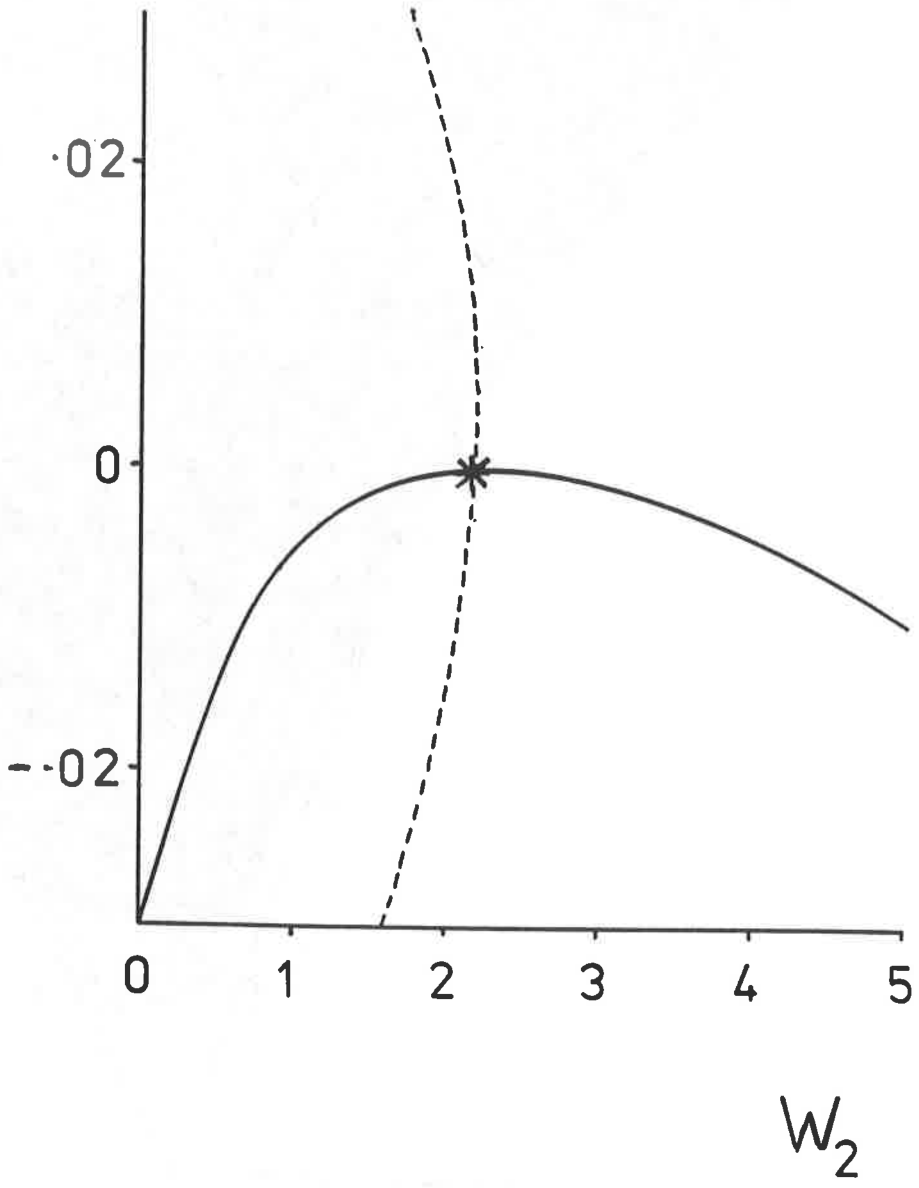
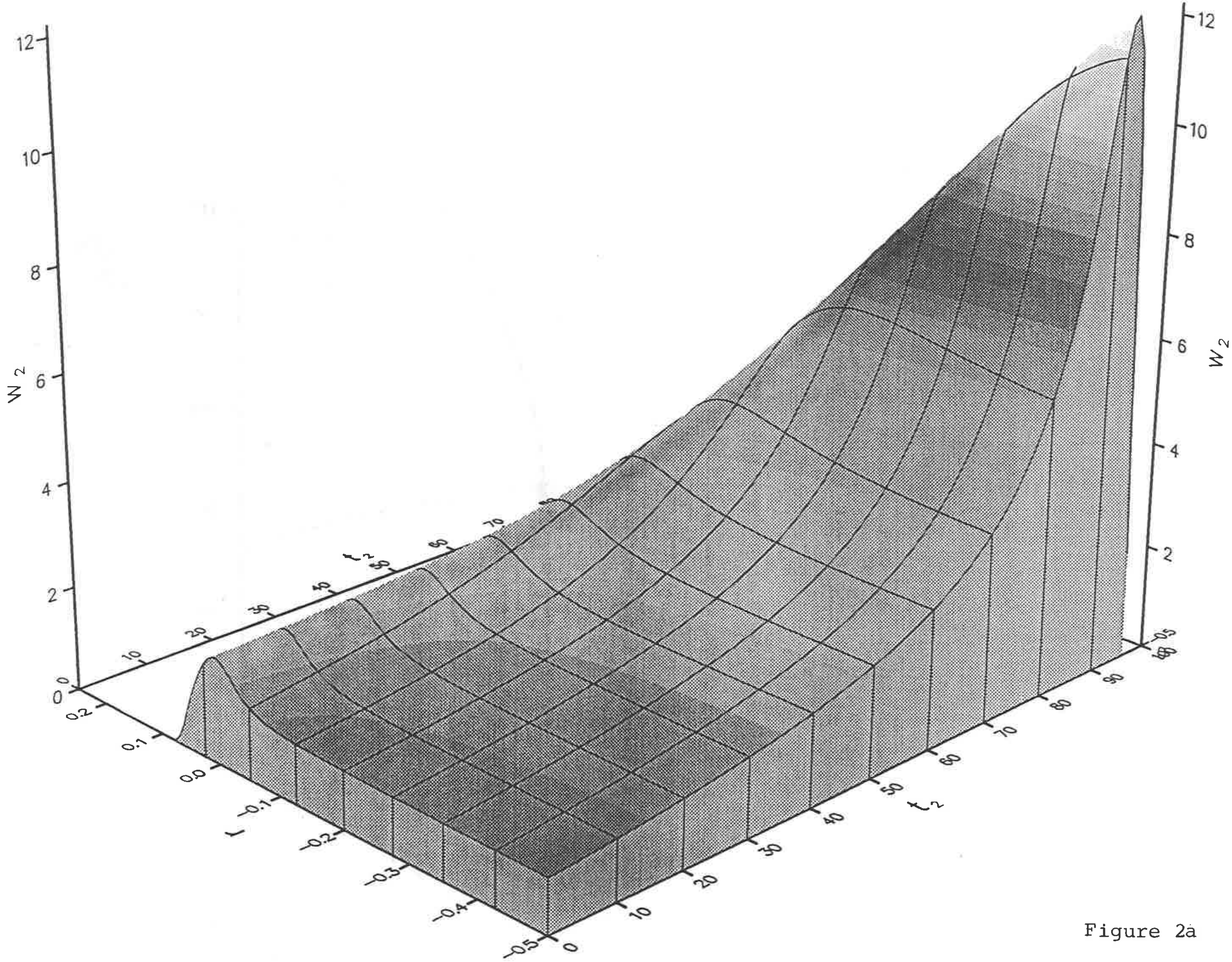


Figure 1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8
6
4
2
0
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0.1
0.0
−0.1
r
−0.2
−0.3
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−0.5
t 2
0
10
20
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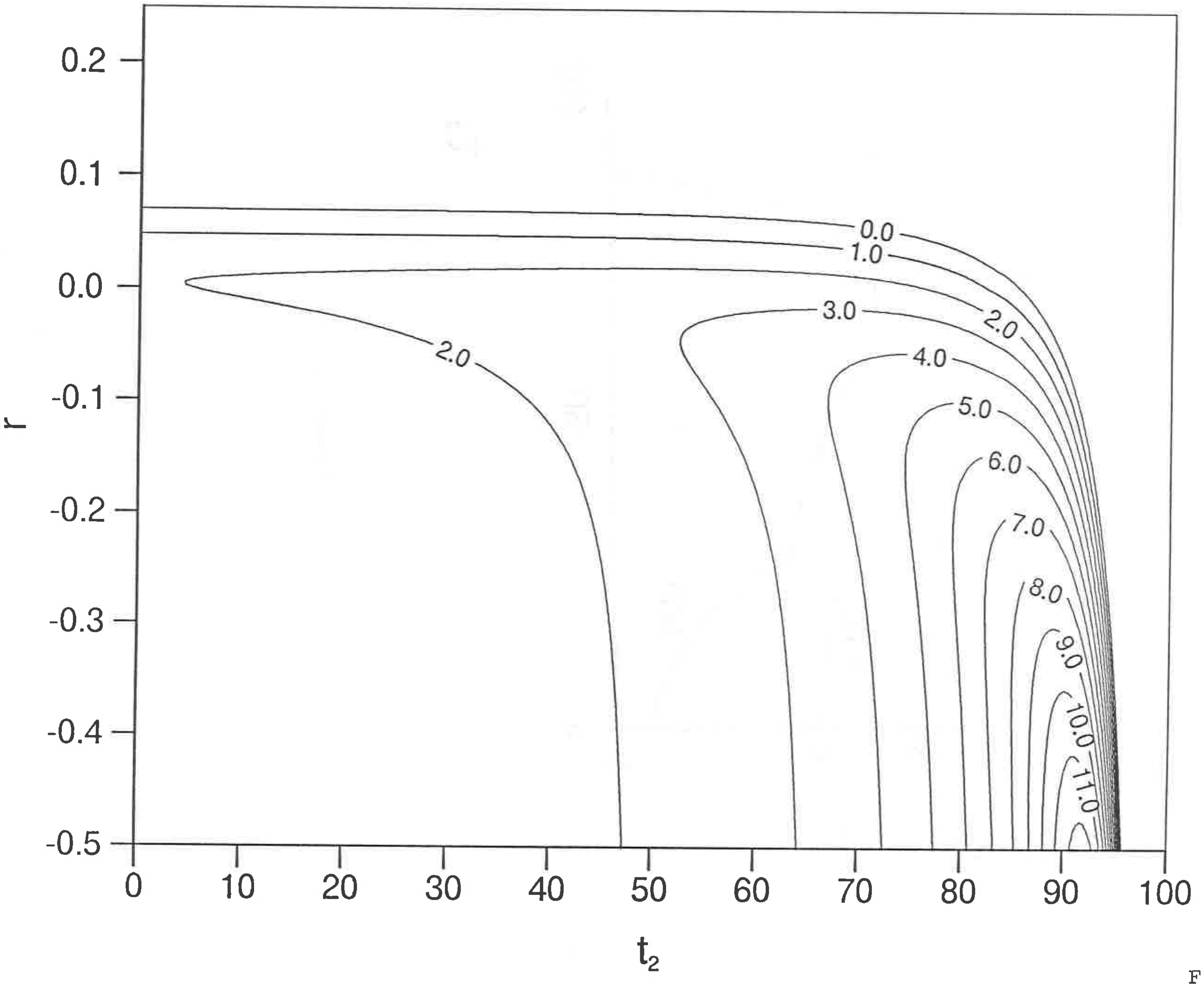
70
80
90
100

Figure 2a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r
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10
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40
50
60
70
80
90
100
t_2
0.0
1.0
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7.0
8.0
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10.0
11.0

Figure 2b

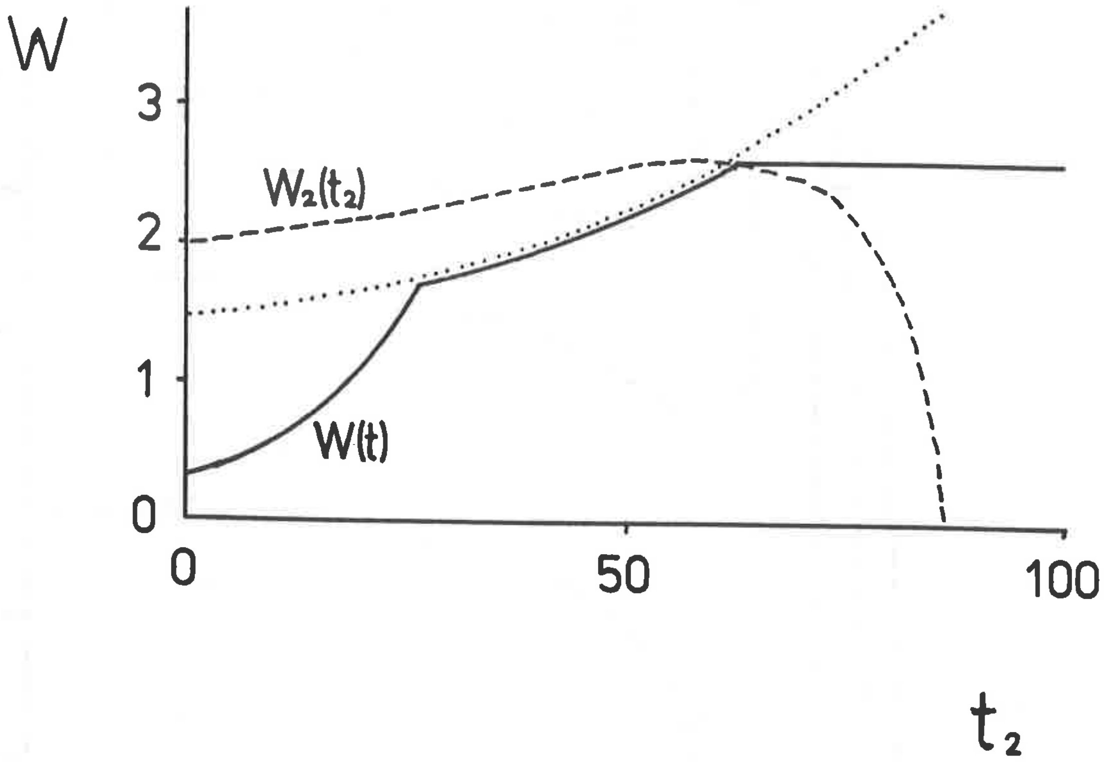

Figure 3

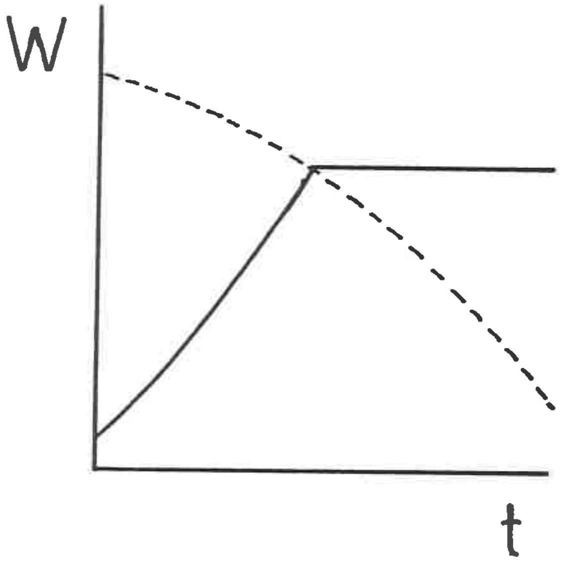

Figure 4a

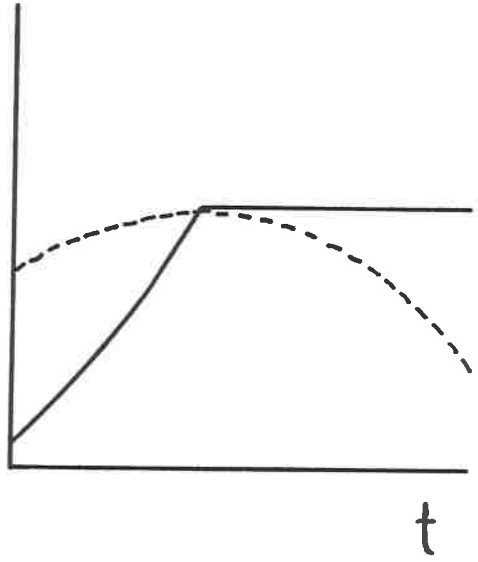

Figure 4b

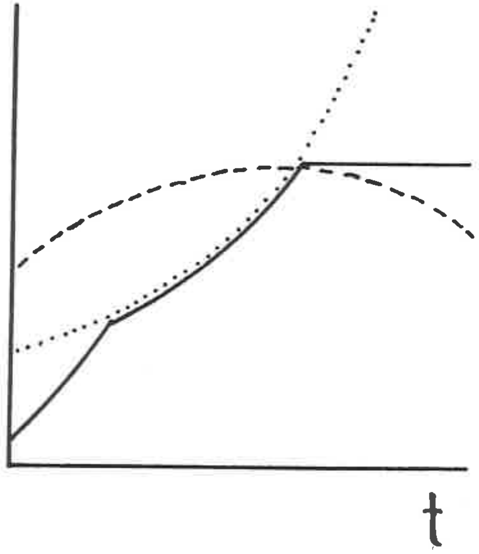

Figure 4c