

# Allocation of energy between growth and reproduction: The Pontryagin Maximum Principle solution for the case of age- and season-dependent mortality

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## ABSTRACT

Optimal allocation of energy to growth and reproduction was studied with a dynamic optimization method for long-lived animals inhabiting a seasonal environment. We found that, after maturation, it is optimal to grow either over several years (if the animals age in the sense that their mortality increases with age) or asymptotically (if there is no ageing). Asymptotic growth can be well approximated with Bertalanffy's equation, even if the animals are able to grow to infinity. This is because it is optimal to allocate an increasing proportion of surplus energy to reproduction year after year following maturation. Age at first reproduction depends on mortality in both favourable and unfavourable seasons, and also depends on the favourable season length – it is optimal to mature early when mortality is high in either season or the season is short. Size at maturity depends additionally on the parameters of the equation describing the size-dependence of the production rate. When mortality in the unfavourable season is high compared to mortality in the favourable season, a large part of growth is realized after maturation. The model qualitatively explains growth patterns and life histories in fish, reptiles, amphibians and some long-lived invertebrates which grow after maturation. To understand better the diversity of life histories, field biologists working on such animals should focus on differences in the ageing rate, favourable season length, mortality rates in both seasons and the size-dependence of production rate. Optimization models based on the allocation principle are promising tools to integrate these kinds of data.

*Keywords:* age at maturity, Bertalanffy's growth curve, life-history evolution, optimal resource allocation, Pontryagin Maximum Principle, seasonality.

## INTRODUCTION

Most fish, reptiles, amphibians and many invertebrates grow intensively after maturation. They differ in their ages at maturity, fractions of maximum size attained at maturity, sizes at maturity, and also the final sizes towards which they grow (often asymptotically). These differences may be observed between related species as well as between local populations within a species. Animals with indeterminate growth are often long-lived and they inhabit

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seasonal environments, with the year divided into productive seasons in which growth and/or reproduction is possible and unfavourable seasons in which physiological processes slow down and neither growth nor reproduction occurs.

Growth in fish, amphibians and reptiles is most often described by Bertalanffy's equation in the form:

$$l_t = l_\infty [1 - e^{-k(t-t_0)}] \quad (1)$$

where  $t$  is age,  $l_t$  is body length at age  $t$ ,  $l_\infty$  is asymptotic length,  $k$  is the growth constant and  $t_0$  is the hypothetical age at which length equals zero (e.g. Charnov, 1993). Although Bertalanffy's equation usually fits the field data, Bertalanffy's original assumption that growth stops because anabolism is offset by catabolism is not justified. This is because animals must have anabolism greater than catabolism to produce offspring tissues (Kozłowski, 1996; Day and Taylor, 1997; Czarnoleski and Kozłowski, 1998). It seems reasonable, therefore, to look to changes in resource allocation to explain slowing growth.

In comparative studies on fish, Beverton and Holt (1959) showed mortality to be positively correlated with Bertalanffy's growth constant. Length at maturity was positively correlated with asymptotic length from Bertalanffy's equation; his growth constant was negatively correlated with asymptotic length. In several papers (Charnov, 1991; Charnov and Berrigan, 1991a,b), summarized by Charnov (1993), a model in which selection acts on age at maturity alone was developed to explain these patterns. Bertalanffy's growth equation is one assumption of Charnov's model. Roff (1983) suggested earlier that Bertalanffy's curves may result from increasing proportions of energy allocated to reproduction when an animal grows older. However, without seasonality, optimization models predict that growth should stop at maturation and reproductive allocation should be constant thereafter (Ziółko and Kozłowski, 1983; Perrin and Sibly, 1993). Kozłowski and Uchmański (1987) built an optimization model in which selection acts on resource allocation during the entire life in a seasonal environment. To get an analytical solution using basic calculus, they had to assume that mortality is constant during life, with additional age-independent mortality occurring during unproductive seasons. Indeterminate growth was found to be optimal, and the growth curves resulting from optimal energy allocation resembled Bertalanffy's curves despite the animals' energetic potential to grow to infinity. More recently, using a similar model with constant yearly survival, Kozłowski (1996) showed that the interspecific patterns of life histories discovered by Beverton and Holt (1959) can result from optimal allocation of resources to growth and reproduction, based on the assumption that the parameters describing mortality, the size-dependence of production rate and the season length differ randomly between species or local populations.

In the present paper, the Pontryagin Maximum Principle, the most advanced tool of dynamic optimization, is applied to find the optimal schedule of energy allocation when mortality differs seasonally and is age-dependent. This method can be used to study optimal allocation patterns under age-specific mortality. Several numerical examples are presented to show how such parameters as season length, maximum life span, the age-dependence of mortality and the size-dependence of the production rate shape the life histories of indeterminate growers living in a seasonal environment. The reasons why achieved growth follows Bertalanffy's equation despite the potential ability to grow linearly or even faster are also discussed.

After introducing the model, numerical examples showing the effect of different parameters on the optimal schedule of growth and reproduction are presented. Then we

present the circumstances in which optimal growth curves should resemble Bertalanffy's curves. Finally, we discuss our results.

### THE MODEL

We consider the problem of the growth–reproduction trade-off for animals living more than 1 year in a seasonal environment (Kozłowski and Uchmański, 1987; Budilova *et al.*, 1995; Kozłowski, 1996). Each season is divided into two parts: a productive season of length  $S$  when growth or reproduction can occur, and a non-productive season – winter or drought – of length  $V$  when neither growth nor reproduction are possible. It is supposed that the animals retain all their vegetative tissues to the next productive season. Storage is not assumed explicitly, but we can bracket the part of the productive season necessary to store fat for winter and treat it as a part of winter. The productive season is considered to be uniform with respect to the adults' performance and offspring survival; that is, offspring produced at any time of the season are of the same quality. It is also assumed for simplicity that the energy allocated to reproduction is released immediately.

Let  $q_A(t)$  denote that part of mortality dependent on age but not dependent on season. An additional season-dependent mortality  $q_{SV}(t)$  occurs, taking a value  $q_S(t)$  in the productive season and value  $q_V(t)$  in winter. Thus total mortality is

$$q(t) = q_A(t) + q_{SV}(t)$$

and the survivorship function  $L(t)$  taking into account both causes of mortality is

$$L(t) = e^{-\int_0^t q(x) dx} \quad (2)$$

Note that  $t$  plays two roles in our model: that of time in the strict sense of the word, and that of age.

Let us suppose that the energy production rate of an individual at size  $w$  (in energy units) is some known function  $f(w)$ . A fraction  $u = u(t)$  of energy is allocated to reproduction at age  $t$ , so that the rate of reproduction at this age measured in units of energy is  $u(t)f(w(t))$ . The remaining surplus energy is allocated to growth, so that the rate of growth is:

$$\frac{dw}{dt} = [1 - u(t)]f(w(t)), \quad w(0) = w_0 \quad (3)$$

If  $u$  was known to be a function of  $t$ , the differential equation (3) could be solved for any initial size  $w_0$ ; that is,  $w$  could be determined as a function of  $t$ . In this case, we could calculate the lifetime reproductive success of an individual,

$$R = \int_0^T u(t)f(w(t))L(t)dt \quad (4)$$

where  $T = (N - 1)(S + V) + S$  is its maximum lifespan and  $N$  is the maximum number of seasons the animals can live.  $R$  is a proper measure of fitness if the population is at equilibrium and if density-dependence acts early in life (Kozłowski, 1993; Mylius and Diekmann, 1995).

The problem here is to construct the control variable  $u$  as a function of  $t$  in such a way that the functional (4) is maximized, taking into account the state equation (3), which can be considered a constraint imposed on the dynamics of the state variable  $w$ . The problem of finding the  $u(t)$  that maximizes (4) can be solved using the Pontryagin Maximum Principle

(Pontryagin *et al.*, 1962), which has already been successfully applied to the growth–reproduction trade-off problem (Ziółko and Kozłowski, 1983; Perrin *et al.*, 1993), but only for non-seasonal environments. The Hamiltonian

$$H = u(t)f(w(t))L(t) + z(t)[1 - u(t)]f(w(t))$$

or, equivalently,

$$H = f(w(t))\{u(t)[L(t) - z(t)] + z(t)\} \quad (5)$$

considered as a function of  $u$  should be maximized for any fixed  $t$  (and consequently for fixed  $w(t)$ ). Control variable  $u(t)$  found this way will be the solution to the optimization problem because it maximizes the functional (4). The so-called adjoint (or co-state) variable  $z$  in the Hamiltonian is defined by a differential equation with the right-hand side equal to the partial derivative of  $H$  in respect to  $w$  taken with a minus sign,

$$\frac{dz}{dt} = -f'(w(t))\{u(t)[L(t) - z(t)] + z(t)\}, \quad z(T) = 0 \quad (6)$$

where

$$f'(w(t)) = \frac{df(w)}{dw}$$

From (5) we see that  $u$  can take only one of two values, 0 or 1, for any fixed  $t$  to maximize  $H$ , because the partial derivative of  $H$  with respect to  $u$  does not depend on  $u$ . Namely, the following condition must be fulfilled:

$$u(t) = \begin{cases} 1 & \text{if } L(t) > z(t) \\ 0 & \text{if } L(t) < z(t) \end{cases} \quad (7)$$

So the problem boils down to solving a system of two differential equations, (3) and (6), with the corresponding boundary conditions taking into account condition (7).

If this system was solved for all possible initial conditions  $w_0$ , then it would be possible to calculate the value of  $z(t, w(t))$  for different points  $(t, w)$  of the state space and so to build the surface  $z(t, w)$ . Then we would have two surfaces over the plane  $(t, w)$  for all  $w$ : the surface for  $L(t, w)$  and the one for  $z(t, w)$ . In this case, to find  $u(t, w)$  at any point of the state space  $(t, w)$ , it would be sufficient to compare the values of  $L(t, w)$  and  $z(t, w)$  and ascribe to  $u(t, w)$  the value 0 or 1 given by condition (7). The problem is that the shape of  $z(t, w)$  itself depends on  $u$ , so finding  $z(t, w)$  is not straightforward.

The problem will be solved if we build the surface  $z(t, w)$ . This can be done proceeding backwards from the terminal time  $T$  to the initial time  $t = 0$ . Let us consider an arbitrary  $i$ th season – that is, the time period between  $t = (i - 1)(S + V)$  and  $t = T_i = (i - 1)(S + V) + S$ . We may set  $u(T_i) = 1$  for any size  $W = W(T_i)$ , positing that this holds for some period of time (perhaps equal to 0) before  $T_i$ , say between  $t_w$  and  $T_i$  (Ziółko and Kozłowski, 1983). In this period there is no growth ( $u(t) = 1$ ), and size is constant and at its maximum ( $w(t) = W$ ). The problem of finding  $z$  for the interval  $t_w < t < T_i$  is not difficult because  $w$  is constant in this interval, and  $u(t)$  is also constant and equal to 1. Hence the differential equation (6) for  $z$  is reduced to the form:

$$\frac{dz}{dt} = -f'(W)L(t), \quad z(T) = 0$$

Integrating this equation through the period from  $t_w$  to  $T_i$  we obtain

$$z(T_i, W) - z(t, W) = -f'(W) \int_t^{T_i} L(x) dx$$

or

$$z(t, W) = z(T_i, W) + f'(W) \int_t^{T_i} L(x) dx \quad (8)$$

and, in particular,

$$z(t_w, W) = z(T_i, W) + f'(W) \int_{t_w}^{T_i} L(x) dx \quad (9)$$

According to equation (7), the following relation is true for the switching point  $t = t_w$ :

$$z(t_w, W) = L(t) \quad (10)$$

Equating the right-hand sides of equations (9) and (10) we obtain an equation enabling us to calculate  $t_w$ :

$$z(T_i, W) + f'(W) \int_{t_w}^{T_i} L(x) dx = L(t) \quad (11)$$

For some  $W$ , condition (11) is not reached before the beginning of the  $i$ th season. This means that equation (8) can be used to calculate  $z(t, W)$  for the entire season. But for some other  $W$  we may obtain  $t_w > (i-1)(S+V)$ , and in this case the backward procedure should be continued using equation (3) with  $u(t) = 0$ , which in this case takes the form:

$$\frac{dw}{dt} = f(w(t)), \quad w(t_w) = W \quad (12)$$

Solving this equation backwards we will find the solution for  $w(t)$  from the beginning of the last season until  $t = t_w$ . Inserting this solution into (6) with  $u(t) = 0$ , we obtain:

$$\frac{dz}{dt} = -f'(w(t))z(t), \quad z(t_w) = z(t_w, W) \quad (13)$$

Solving (13) we find  $z$  for all  $t$  from  $(N-1)(S+V)$  until  $t = t_w$ , in particular for the beginning of the last season. Thus the surface  $z(t, w)$  can be found for the last season both for that part of the plane  $(t, w)$  where  $u = 0$  and for the remainder of the plane  $(t, w)$  where  $u = 1$ .

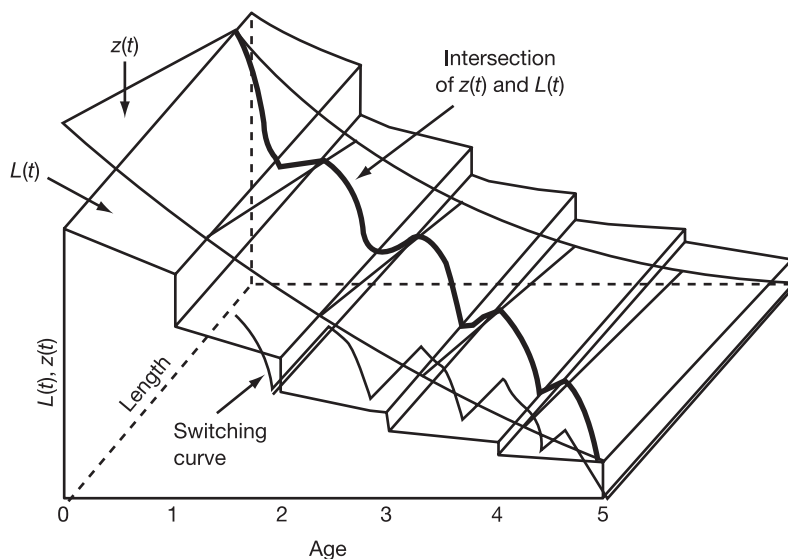
Because neither growth nor reproduction is possible in winter, we can omit winters from here on because  $z$ , as it follows from (6), always remains constant during winter.  $L(t)$  becomes step-like at the end of the productive season after winter is cut out of the time axis.  $L$  versus  $z$  would not change if winter was not cut out: although  $L(t)$  would not be step-like at the beginning of the productive season,  $z(t)$  would remain constant during the winter, which gives exactly the same difference between  $L$  and  $z$  at the beginning of the productive season.

Note that, for the last season, in accordance with (6), the value of  $z(T_N, W)$  in (8) and (9) is 0 for all  $W$ , but for any earlier season  $i$  – when the end of the productive season is not  $T_N$  but  $T_i = (V+S)(i-1) + S$  – the values of  $z(T_i, W)$  are equated to the already calculated values of  $z$  at the beginning of the subsequent season, that is, at  $t = (V+S)i$ . As a result, the backward procedure applied first to the  $N$ th season gives the  $z$  values at the beginning of the next to last season for all  $w$ . The same procedure can then be applied to this season using  $z$  obtained at the beginning of the last season as a terminal boundary condition similar to

condition  $z(T_N) = 0$  used before. Having found the solution for season  $N - 1$ , we can apply the procedure to season  $N - 2$  and so on until the first one, so that finally we build  $z(t, w)$  for all seasons and can find the intersection of  $z(t, w)$  and survivorship  $L(t, w)$  defined by equation (2). The projection of this intersection on plane  $(t, w)$ , the so-called switching curve, divides this plane into two parts: in the first one growth is optimal ( $u = 0$ ), while in the other reproduction is optimal ( $u = 1$ ) (see Fig. 1 for an example).

It is clear from the procedure for finding co-state variable  $z$  that there is no discontinuity in  $z(t, w)$  at the boundaries between seasons after winters are cut out. At the same time, as we have already pointed out, the survivorship function  $L(t, w)$  is discontinuous at these boundaries. But, as follows from (7), we decide whether  $u = 1$  or  $u = 0$  by comparing  $L$  with  $z$ . This means that switchings from  $u = 1$  to  $u = 0$  are possible at the boundaries between seasons for some  $w$  because of a sharp decrease in  $L$ , yielding a saw-shaped switching curve with its 'teeth' at the between-season boundaries. As a consequence, the optimal strategy is characterized by alternating periods of growth and reproduction: in some years the organism grows during the initial part of the productive season and then reproduces up to its end, then again grows during the initial part of the next productive season and reproduces during its remaining part, and so on (see examples in Figs 2–5).

For this procedure, the probability of surviving to a given age  $L(t)$  must be known for the entire life span. If, in addition,  $L(t)$  has some special forms, then it is also possible to find the function  $z(t, w)$  analytically. Two sample cases allowing the problem to be solved analytically will be considered next.



**Fig. 1.** Survival  $L(t, w)$  and co-state  $z(t, w)$  surfaces in three-dimensional space. Production rate is expressed by  $30w^{0.67}$ , where  $w$  is body size in energy units. Instantaneous mortality is 0.4 per year in the favourable season and 0.5 in the unfavourable season. Favourable season length is 50% of the year. Life span is 5 years. For large  $t$  and  $w$  the  $z(t, w)$  surface is below the  $L(t, w)$  surface, and for smaller  $t$  and  $w$  it is above the  $L(t, w)$  surface. Projection of the intersection of these surfaces onto the plane  $(t, w)$  gives the switching curve. To maximize the expected lifetime energy allocation to reproduction, it is optimal to allocate all surplus energy to growth when below the switching curve and to reproduction above this curve.

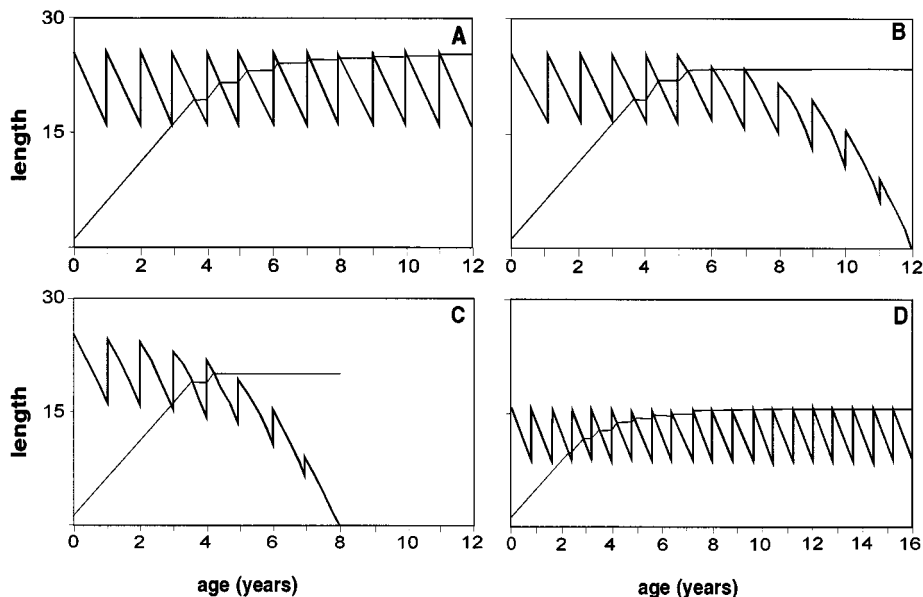
## NUMERICAL EXAMPLES

To illustrate the procedure presented in the previous section, we show the maximum principle solution for a case in which the production rate  $f(w)$  is given by a power function of  $w$ :

$$f(w) = aw^b \quad (14)$$

Productive season length is expressed as a fraction of a year.

Let us first consider the case, similar to the one given by Kozłowski and Uchmański (1987), in which the mortality rate is only season-dependent and not age-dependent. The expressions for the probability of surviving to a given age and for  $z(t,w)$  are given in Appendix 1. The productive season length is set at 0.5. The instantaneous mortality rate in this season is 0.4 per year (equivalent to a 0.82 probability of surviving this season) and 0.5 in the unproductive season (equivalent to a 0.78 probability of surviving this season). The production rate equals  $f(w) = 30w^{0.67}$ . Figure 2A shows the optimal solution for the first 12 years of an unlimited life span. The switching curve has a saw-shaped form which leads to alternating periods of growth and reproduction. Because growth is optimal below the switching curve and reproduction is optimal above it, the optimal strategy in this example is to grow during three whole seasons and during the first part of the fourth season, then reproduce up to the end of the fourth season, grow again at the beginning of the fifth season and reproduce during the rest of it, and so on. All the teeth on the switching curve are the same size. The optimal growth curve crosses the switching curve in the middle of the fourth



**Fig. 2.** The effect of life span and favourable season length on the optimal switching curve (bold line) and growth curve (thin line). Instantaneous mortality is 0.4 per year in the favourable season and 0.5 in the unfavourable season. Favourable season length is 50% of the year for (A) to (C) and 30% for (D). Life span is unlimited for (A) and (D), 12 years for (B) and 8 years for (C). Production rate is the same as in Fig. 1. Winters are cut out of the time axis.

productive season, and closer and closer to the beginnings of consecutive years. This causes growth to slow down with age. Growth is asymptotic, however, and never stops completely when the life span is unlimited. The length attained at maturity equals 72% of final size.

Figure 2B presents the switching and the optimal growth curves for a life span limited to 12 years, and Fig. 2C the curves for a life span of 8 years. The teeth on the switching curves become smaller and go down towards the end of life. This is because the time horizon shortens with age, which makes investments in growth less profitable. This change in the shape of the switching curves has a qualitative effect on the optimal growth curves. Growth not only slows down with age but even stops completely after several years (after 7 years for a 12-year life span, and after 5 years for an 8-year life span).

Figure 2D shows the effect of decreasing the length of the productive season to 30% of the year. The switching curve is now positioned lower than for a 50% productive season length. Maturity appears earlier in the second year, which leads to smaller size at maturity. Final size is also much lower. The proportion of maximum size attained at maturity is higher under a shorter productive season: 61% of final size.

Figure 3 illustrates the effect of mortality on the optimal growth curves. Figure 3A is repeated (for reference) with the same parameters as in Fig. 2A. Mortality in the unfavourable season is increased from 0.5 to 1.0 in Fig. 3B (which is equivalent to a 0.61 probability of winter survival). The saw-shaped switching curve is positioned lower on the graph. Because the peak values of the teeth define the maximum length of the organism, the growth curve in Fig. 3B leads to a much lower maximum size compared to Fig. 3A. The lowest position on the teeth defines the lowest possible size at maturity (in fact, this size is usually slightly higher, because the growth curve is unlikely to cross the switching curve at the lowest allowable position). Thus the ratio of the base to the peak of a tooth is the lower limit of the fraction of maximum body length attained at maturity. This ratio is smaller under higher mortality in the unfavourable season. This is reasonable: if surviving to the next season is unlikely, investments expected to be paid back later are less profitable. This makes earlier maturation (in the second year, not in the fourth as in Fig. 3A) and more investment in reproduction in each succeeding year optimal.

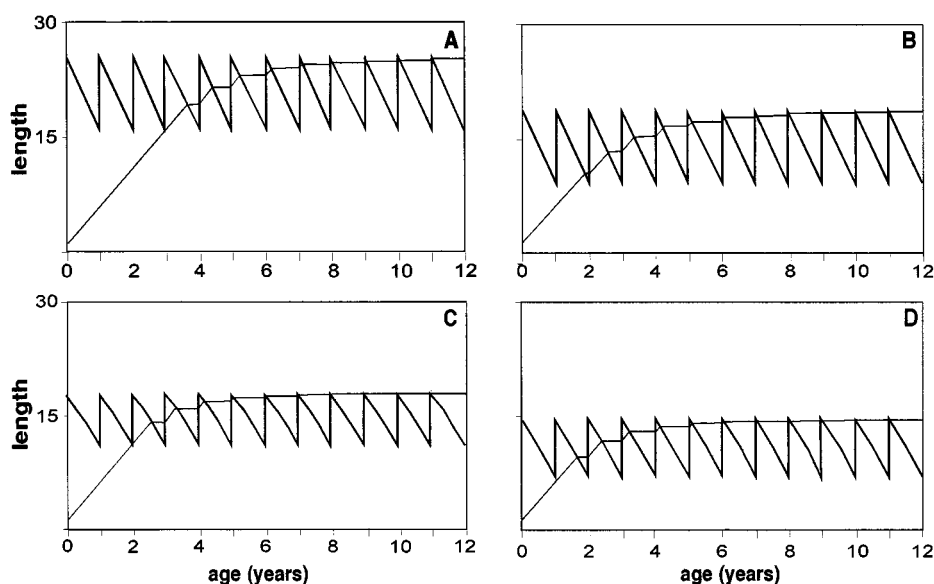
Figure 3C shows the optimal solution when mortality in the favourable season is increased to 0.8 (summer probability of survival equal to 0.67) and winter mortality is left at 0.5. Such a case can be expected if the animals are safer when inactive during winter. The switching curve is also positioned lower than in Fig. 3A, but the teeth are short and non-linear. The low tooth base/pick means that the optimal trajectory of growth produces small animals which attain a large proportion of maximum size before maturation. Figure 3D illustrates the case with a high mortality rate in both seasons (0.8 and 1.0, respectively). The animals mature at a very small size and attain a very small final size if mortality is high in both seasons.

To illustrate the effect of ageing, a particular case of the age-dependent component of mortality given by the expression

$$q_A = q_0 \frac{T}{T-t} \quad (15)$$

was assumed, where  $T$  is maximum longevity. The mortality rate defined this way increases with age and tends to infinity when  $t$  approaches  $T$ . For values of  $q_0$  very close to zero, age-dependent mortality is very low for almost the entire life span and goes quickly to infinity



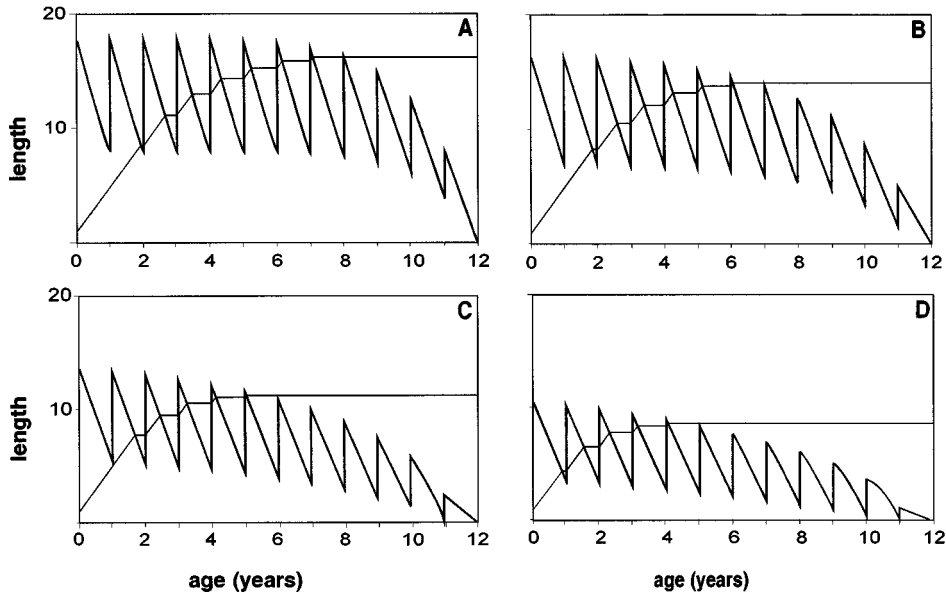


**Fig. 3.** The effect of mortality on the optimal switching and growth curves. Instantaneous mortality is: (A) 0.4 per year in the favourable season and 0.5 in the unfavourable season, (B) 0.4 and 1.0, (C) 0.8 and 0.5 and (D) 0.8 and 1.0. Other parameters as for Fig. 2A.

at the end of life. When  $q_0$  increases, age-dependent mortality increases earlier in life. Expressions for the probability of surviving to a given age and for  $z(t, w)$  are given in Appendix 2. We assumed that age-dependent mortality is the only source of favourable-season mortality and that the instantaneous mortality rate in the unfavourable season equals 1.0 (which means a 0.55 probability of survival). The production rate parameters were the same as in the previous examples.

The switching and optimal growth curves for the case with  $q_0$  close to zero are shown in Fig. 4A. Figures 4B, 4C and 4D show the switching curves and growth curves for  $q_0$  equal to 0.05, 0.2 and 0.5, respectively. There are two effects of increased  $q_0$ : (1) the switching curve is positioned lower from the beginning of life because mortality increases in general, and (2) the effect of ageing makes the teeth shorter and makes them go down earlier in life. As a result, maximum size decreases and maturation appears earlier. When  $q_0$  increases to 0.2, maturation is shifted towards the beginning of the second year, and the proportion of maximum length attained at maturity increases from 0.52 to 0.68 (Figs 4A–C). When  $q_0$  is increased further to 0.5, maturation is shifted to the first year; the proportion of maximum length attained at maturity falls back to 0.52 (Fig. 4D). So size at maturity as well as the proportion of maximum size attained at maturity may change non-linearly as functions of  $q_0$ .

The effects of season length and mortality on the switching and growth curves are shown in Figs 2–4. Figure 5 shows the effect of the production parameters in equation (14) on the growth curves, mainly showing when growth before maturation is expected to be linear if size is measured as length. Figure 5A repeats Fig. 2A, with production rate  $f(w) = aw^b = 30w^{0.67}$ . Note that the growth curve before maturation is linear. Figure 5B shows the optimal



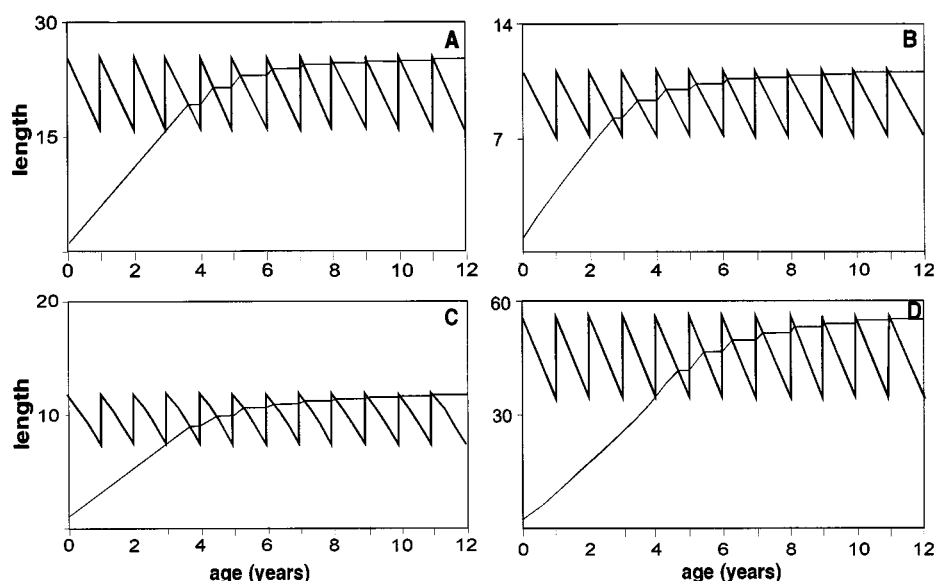
**Fig. 4.** The effect of age-dependent mortality on the optimal switching and growth curves. Life span is limited to 12 years. Instantaneous mortality changes with age according to equation (15), with  $q_0$  equal to 0.0001 (A), 0.05 (B), 0.2 (C) and 0.5 (D). Higher  $q_0$  means earlier effects of ageing, but for all values the mortality rate reaches infinity at maximum life span. Additional age-independent mortality is assumed in the unfavourable season with an instantaneous rate of 1.0 per year. Other parameters as for Fig. 2A.

solution with the exponent of production equation decreased to 0.62, and Fig. 5D with the exponent increased to 0.72. The growth curve will always be linear before maturation if size is expressed as  $w^{1-b}$ . Because length is roughly proportional to body weight to the power 1/3, the growth curve expressed as length is linear for  $b = 2/3$  (Fig. 5A), concave downward for  $b < 2/3$  (Fig. 5B) and concave upward (convex) for  $b > 2/3$  (Fig. 5D). Age at maturity as well as size at maturity increases with the exponent. Figure 5C shows the optimal solution with production rate expressed by  $20w^{0.67}$ . Note that we obtain a proportional dwarf of the case shown in Fig. 5A, maturing at the same age but at a much smaller size, and having a much smaller final size.

### PREDICTED VERSUS BERTALANFFY GROWTH CURVES

The growth asymptote is one of the Bertalanffy equation parameters. The growth curve generated by our model under unlimited maximum life span (for example, see Fig. 2A) also asymptotically approaches some limiting size  $w_\infty$ . In fact, this limiting size coincides with the height of the switching curve teeth as presented in Fig. 2A. In Appendix 3, the following formula for  $w_\infty^{1-b}$  is obtained for season-dependent but age-independent mortality:

$$w_\infty^{1-b} = \frac{2a(1 - e^{-q_s S})}{3q_s(1 - e^{-(q_s S + q_v V)})} \quad (16)$$



**Fig. 5.** The effect of the parameters of the production equation  $f(w) = aw^b$  ( $w$  = body size in energy units) on the optimal switching and growth curves under unlimited life span. Constant  $a$  equals 30 for (A), (B) and (D), and 20 for (C). Exponent  $b$  equals 0.67 for (A) and (C), 0.62 for (B) and 0.72 for (D). Other parameters as for Fig. 2A.

This expression gives the relation between parameters  $a$ ,  $q_S$ ,  $q_V$ ,  $S$ ,  $V$  and asymptotic size, which is proportional to parameter  $a$  in the equation determining the production rate and inversely proportional to summer mortality  $q_S$ . If  $q_V = 0$  or  $V = 0$  (no winters or no winter mortality), then  $a$  and  $q_S$  completely determine  $w_\infty^{1-b}$ , but if  $q_V V$  is greater than 0, then  $w_\infty^{1-b}$  is also proportional to the ratio of the probability of dying in summer to the probability of dying in the entire year. That is, the longer and more severe winters are, the lower the asymptotic size of the animals.

The next question is whether our optimal growth curve may be approximated by the Bertalanffy curve (1) when discontinuities in growth are omitted. Here we consider only the case with  $b = 2/3$ , when  $l_\infty$  is equivalent to  $w_\infty^{1-b}$ . It is easy to show that the subsequent annual increments in length would experience a decreasing geometric progression (that is, the growth curve would be Bertalanffy-type) if the seasonal fragments of the switching curves were rectilinear. But are they? Strictly speaking they are not, because these fragments are portions of curves bounded by the constant  $2a/3q_S$ . Nevertheless, the final parts of the switching curves for consecutive seasons are sufficiently close to the segments of a straight line, as can be seen in Figs 2–4 (except Fig. 3C). Thus the optimal growth curves (not counting discontinuities) do not coincide with Bertalanffy's growth curves but can be well approximated by these curves for a broad range of parameters. When  $a$  is very small,  $q_S$  is very big or  $q_V$  is relatively small (as in Fig. 3C), the switching curves are far from rectilinear, and Bertalanffy's approximation is much worse: one can observe a slower decrease in annual length increments at the beginning of life and a faster decrease at older ages, resulting in a fast approach to the limit on length during the few first years of life.

When the production rate exponent is greater than  $2/3$  (Fig. 5D), Bertalanffy's curve will approximate the optimal growth curve with size expressed by  $w^{1-b}$ , but for size expressed by length the optimal growth curve before maturation grows faster than linearly.

For limited life span or mortality increasing with age, the teeth on the switching curve decrease with age, rapidly so close to the end of life. This causes growth to stop completely after several years without approaching the final size described by equation (16). We must remember, however, that the growth curve will approach the one defined by Bertalanffy's equation at the beginning of life, and animals old enough to stop growing are usually so rare that a deviation from Bertalanffy's growth curve may be virtually impossible to discover.

In summary, it is not surprising that Bertalanffy's growth curves usually approximate real growth curves of indeterminate growers. Applying these curves is appropriate as long as they are treated as phenomenological descriptions and one is not trying to interpret the parameters' meanings. Because Bertalanffy's curves result from optimal allocation of resources, they should not be applied as an assumption about growth in optimization models.

## DISCUSSION

The switching curve divides the plane defined by the age and size axes into two parts: it is optimal to grow below the switching curve and to reproduce above it. The switching curve is a straight line parallel to the age axis in an aseasonal environment if the lack of ageing is demonstrated by mortality constant with age (e.g. Kozłowski and Wiegert, 1987; Perrin and Sibly, 1993) or by a monotonically decreasing curve for animals whose mortality increases with age. Thus determinate growth is optimal in an aseasonal environment because an animal which has once crossed the switching curve has no chance of being below it in the future. Seasonality makes switching curves non-monotonic: they decrease during favourable seasons and increase during unfavourable seasons. This means that an animal which has crossed the switching curve and reproduced is likely to be back below the switching curve at the beginning of the next year, which makes growth optimal once more. Such switching curves lead to either (1) indeterminate growth which approaches an upper limit asymptotically, or (2) slowing growth which stops completely after several years. Which is optimal depends on the mortality schedule. If the life span is unlimited and mortality is age-independent, the teeth on the switching curves are of the same shape and size during the animal's entire life, and asymptotic growth is optimal (see examples illustrated by Figs 2A, 2D, 3 and 5). If the life span is limited and/or mortality increases with age, the teeth move down to a lower body size and become smaller towards the end of life. This leads to limited final size. Final size is attained after some years of mixed growth and reproduction, unlike in an aseasonal environment (see examples illustrated by Figs 2B, 2C and 4).

Iwasa and Cohen (1989) applied the Pontryagin Maximum Principle to consider the optimal growth schedule of a perennial plant. Their results contradict ours: perennial plants should not increase their size after maturation. Pugliese (1987, 1988) obtained a similar result using a different mathematical approach. Some perennial herbs behave this way, whereas other herbs, half-shrubs, shrubs and trees do not. It was assumed in these models that only storage organs persist over winter and that other vegetative tissues are lost in autumn. Here we posit that long-lived animals have all vegetative tissues permanently. Indeed, Pugliese and Kozłowski (1990) found that there is a threshold proportion of vegetative organs which must be permanent for indeterminate growth to be optimal. This

proportion is dependent on winter mortality. Some perennial plants do overwinter in the form of storage organs only, whereas others retain main roots, trunks and branches which are not productive organs but need energy to build them. Some plants store energy, at least partly, in roots which are functional organs as well. Thus the results are consistent: perennial plants should or should not grow after maturation, whereas animals, retaining most of their vegetative tissues over winter, should grow intensively after maturation unless some constraints prevent it.

Under optimal allocation of resources, the proportion of time during which energy is allocated to growth decreases steadily after maturation. It produces concave or S-shaped growth curves when linear size (length) is measured and discontinuities in growth are omitted. The production rate was described in the numerical examples by a power function with exponent  $b < 1$  and size measured in energy units. We do not suggest that this equation is universal, but it is flexible enough to approximate a real production equation for a broad range of body sizes. If  $b < 2/3$ , the growth curve for length is concave downward from the beginning of life and can be approximated by Bertalanffy's equation. If  $b = 2/3$ , the growth curve is linear before maturation and concave after; such a curve can also be approximated by Bertalanffy's equation. If  $b > 2/3$ , the growth curve is convex before maturation and concave after maturation; such a curve is better approximated by a logistic growth curve or another curve with an inflection point. Thus the kind of curve that fits the data on growth allows for a qualitative test of the production rate exponent, providing that a test has been made to find which curve fits best. The general use of Bertalanffy's growth equation in the literature seems to show that the exponent  $b$  is usually not greater than  $2/3$ , but in some cases where the average sizes or individual sizes for each age class are given, growth before maturation seems to follow a concave upward pattern (e.g. Read, 1987; Griffiths and Kirkwood, 1995; Booth and Merron, 1996). This suggests that the range of the production rate exponent may be quite broad, sometimes exceeding  $2/3$ .

Age-dependent mortality was assumed in this paper. Whereas it is better than the assumption of constant mortality (Kozłowski and Uchmański, 1987; Kozłowski, 1996), the size-dependence of mortality should also be taken into account. Although the optimality condition (7) is also valid under size-dependent mortality, there are technical difficulties yet to be solved when constructing the  $L$  and  $z$  functions for such mortality. Our guess is that the switching curve should move up if mortality decreases with size, which makes later maturation and larger final size optimal.

The optimal life history of animals growing after maturation can be well defined by (1) age at maturity, (2) age at which growth stops (sometimes infinity), (3) size at maturity and (4) final size. The ratio (3)/(4) measures the proportion of final size attained at maturity. It is difficult to ascertain whether growth stops at some age or is continuous but slows towards the end of life, unless there are age marks as on scales (in fish) or on shells (in molluscs). If one only has measures of age and size, low numbers of old animals together with intraspecific variability precludes a solution. Moreover, the old animals had their intensive growth many years earlier when environmental conditions could have been different. This is another factor in the variability of size among animals. For the same reasons, it is not possible to measure maximum size directly; instead, an asymptote from a fitted growth curve of an assumed form (e.g. Bertalanffy's) is usually applied (e.g. Charnov, 1993).

As shown on pp. 430–432 the switching curve depends on the length of the favourable season, mortality in both parts of the year, ageing, and the parameters of the production

equation. It is not easy to find all these parameters for any natural population, but knowledge of life-history parameters allows us to make qualitative predictions that are useful for comparative purposes. Optimal asymptotic final size is positively related to the production parameters and to the ratio of the probability of dying in a favourable season to the probability of dying throughout the entire year, and negatively related to the favourable season mortality rate. Optimal age at maturity is independent of production constant  $a$  but is strongly dependent on production exponent  $b$ . A large part of growth should be realized after maturation if survival over unfavourable seasons is low, which means long unfavourable seasons and/or a high mortality rate during them. One must remember, however, that optimization models provide information about selection pressures only, and not about the outcome of selection, which also depends on the genetic structure of a population (e.g. Maynard Smith, 1978). It is likely that natural selection does not act directly on the above life-history features but rather on the plastic response to food conditions and mortality indicators. This means that individuals may adjust their life histories to the conditions they encounter. Under size-independent changes of food conditions (the constant  $a$  in production equation (14) changes), animals should mature at the same age but different sizes, which are, however, constant proportions of final sizes. If food conditions improve more for larger animals (which means an increase of the exponent in the production equation), maturation should be delayed. Any stress or other sign indicating an increase in mortality should cause earlier maturation at a smaller size. Because the mortality risk cannot be perceived by animals as precisely as food conditions can, we should expect much more genetic variability for the plastic response to mortality than to productivity.

Recently, Trippel (1995) surveyed the literature on the effect of intense exploitation on age at maturity in fish. In almost all populations which declined because of harvesting (sometimes dramatically), age at maturity decreased, often by more than 40%. Usually size at maturity also decreased. These changes are rapid considering the long generation time of these fish, which suggests that the plastic phenotypic response is more important than genetic changes. Trippel used a compensation hypothesis to explain this decrease in age of maturation, which states that a population decline releases intraspecific competition, results in faster growth and speeds maturation. This explanation is unsatisfactory because of the simultaneous decline in size at maturity. The compensation hypothesis assumes that size at maturity is more conservative than age at maturity under improved food conditions. Such a reaction seems non-optimal according to the model presented here (compare Figs 5A and 5D), which predicts decreases in both size and age at maturity as most often observed in nature. Compensatory improvement in food conditions may also take place: Trippel reported cases in which age at maturity declined and size did not. It is likely, however, that in most cases the food conditions did not improve significantly, possibly because of competition with other species that matured at an earlier age and thus were better able to tolerate intensive harvesting.

It appears that heavily harvested fish respond to the increased risk of mortality. Which signal of increased mortality is sensed by the fish? Low density and low numbers of old conspecifics are among the best candidates. Kasperski and Kozłowski (1993) observed maturation at smaller size (and probably lower age) in exploited laboratory guppy populations. Field data also support the importance of this cue in fish (e.g. Baccante and Reid, 1988; Belk, 1995).

The proportion of final size attained at maturity is in the range 0.40–0.88 for different groups of fish (Beverton, 1992), 0.6–0.8 for turtles (Shine and Iverson, 1995) and 0.4–0.9

for snakes and lizards (Shine and Charnov, 1992). Age at maturity is also quite variable in nature. The broad ranges of these life-history parameters could indicate high variability of season length and/or mortality during favourable and unfavourable seasons. Size varies enormously between different species of fish. This means that production rates also vary widely. Such a wide range in size observed in nature could not be explained if only mortality parameters varied, as basically assumed by Charnov (1993).

In this paper, the mortality rate was assumed to be age-dependent. However, Teriokhin (1997) obtained Gompertz's type mortality rate dynamics (as in humans and many other animals) as a result of optimal allocation of resources to repair throughout life. Thus, life-history modelling by the resource allocation principle seems a very robust and promising approach.

The model presented here suggests what we should measure in nature to explain the great variability of life histories in indeterminate growers. We should focus on the rate of ageing (age dependence of mortality), length of growing season, mortality rate in growing seasons and winters, and the size dependence of the production rate. Although Bertalanffy's growth curves fit the field data, they should not be used in modelling life-history evolution because such curves result from optimization and cannot be treated as an assumption (Day and Taylor, 1997; Czarnoleski and Kozłowski, 1998). Thus the growth constant from Bertalanffy's equation says nothing about the growth potential implied by the production rate. This rate should be estimated by the sum of the growth and reproduction investments. To understand life-history evolution better, it is necessary to distinguish model assumptions and model predictions precisely. This is possible with life-history optimization models based on the allocation principle.

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## APPENDICES

## 1. Probability of surviving and co-state variable with unlimited life span

Assume that the age-dependent component  $q_A = 0$  and hence the corresponding survival function is

$$L(t) = h^{i-1} e^{-q_S t} \quad (\text{A1})$$

for the  $i$ th productive season, where

$$h = e^{-(q_V V + q_S S)} \quad (\text{A2})$$

and  $t$  is the time elapsed from the beginning of the favourable season  $i$ . Assume for a while that life span is limited to  $N$  years. Remembering that the production rate is described by (14), in this case equation (8) for calculating  $z$  in the  $i$ th season in the region of the  $(t, w)$ -plane with  $u = 1$  takes the form

$$z(t, W) = z(T_i, W) + ab W^{b-1} h^{i-1} \int_t^{T_i} e^{-q_S x} dx \quad (\text{A3})$$

which gives

$$z(t, W) = z(T_i, W) + ab W^{b-1} h^{i-1} \frac{1}{q_S} [e^{-q_S t} - e^{-q_S T_i}] \quad (\text{A4})$$

This formula holds, in particular, for the last season  $N$  after replacing  $i$  with  $N$  and  $T_i$  with  $T = T_N$ . Correspondingly, equation (11) that determines the switching curve separating regions with  $u = 0$  and  $u = 1$  takes the form

$$z(T_i, W) + ab W^{b-1} h^{i-1} \frac{1}{q_S} [e^{-q_S t} - e^{-q_S T_i}] = h^{i-1} e^{-q_S t} \quad (\text{A5})$$

which can be simplified for the last season to

$$t_W = T - \frac{1}{q_S} \log \frac{1}{1 - (q_S / ab W^{b-1})} \quad (\text{A6})$$

After integrating from  $t$  to  $t_W$ , equation (12) describing the dynamics of growth in the region  $u = 0$  gives the following solution:

$$w(t) = [W^{1-b} - a(1-b)(t_W - t)]^{1/(1-b)} \quad (\text{A7})$$

Inserting this solution into equation (6) with  $u(t) = 0$ , we obtain

$$\frac{dz}{dt} = -ab [W^{1-b} - a(1-b)(t_W - t)]^{-1} z(t), \quad z(t_W) = z(t_W, W) \quad (\text{A8})$$

Solving this equation, we obtain the expression

$$z(t, w(t)) = z(t_W, W) \left( \frac{W}{w(t)} \right)^b \quad (\text{A9})$$

which can be used for determining  $z$  for all  $t$  from  $(i-1)(S+V)$  until  $t = t_W$ , in particular for the beginning of the  $i$ th season.

Having found  $z$  for the last season, proceeding backwards we can find the solution for  $z$  and the corresponding switching curve for the preceding season and then for still earlier ones. Because  $N$  does not appear in (A9), we can assume any value for it, including infinity.

## 2. Probability of surviving and co-state variable with sample age-dependent mortality

Let us now assume that the age-dependent component of mortality equals:

$$q_A(t) = q_0 \frac{T}{T-t} \quad (\text{B1})$$

The survivorship function corresponding to that component of mortality would be

$$L_A(t) = e^{-\int_0^t q_0 T/(T-s) ds} = \left(\frac{T-t}{T}\right)^{q_0 T} \quad (\text{B2})$$

We assume that the summer component of mortality  $q_S$  is 0. Then the probability of surviving to age  $t$  defined by equation (2) for the  $i$ th productive season becomes

$$L(t) = h^{i-1} \left(\frac{T-t}{T}\right)^{q_0 T} \quad (\text{B3})$$

where  $h$  is defined by equation A2. In the same way as in Appendix 1, we obtain the following expression for  $z$  for the  $i$ th season:

$$z(t, W) = z(T_i, W) + abW^{b-1} h^{i-1} \int_t^{T_i} \left(\frac{T-x}{T}\right)^{q_0 T} dx \quad (\text{B4})$$

which gives the expression

$$z(t, W) = z(T_i, W) + abW^{b-1} h^{i-1} \frac{T}{1+q_0 T} \left[ \left(\frac{T-t}{T}\right)^{1+q_0 T} - \left(\frac{T-T_i}{T}\right)^{1+q_0 T} \right] \quad (\text{B5})$$

This holds, in particular, for the last season  $N$  after replacing  $i$  with  $N$  and  $T_i$  with  $T = T_N$ .

Correspondingly, equation (11) that determines the switching curve separating regions with  $u = 0$  and  $u = 1$  takes the form

$$z(T_i, W) + abW^{b-1} h^{i-1} \frac{T}{1+q_0 T} \left[ \left(\frac{T-t}{T}\right)^{1+q_0 T} - \left(\frac{T-T_i}{T}\right)^{1+q_0 T} \right] = h^{i-1} \left(\frac{T-t}{T}\right)^{q_0 T}$$

which can be simplified for the last season to

$$t_W = T - \frac{1+q_0 T}{abW^{b-1}} \quad (\text{B6})$$

The equation describing the dynamics of growth in the region with  $u = 0$  is the same as in Appendix 1.

### 3. Final size with unlimited life span

For any finite life span  $T$  there exists a season  $i$  in which maximum size  $W$  is attained. Hence, for all  $t$  between  $i$  and  $T$ , the dynamics of the co-state variable  $z$  for  $w(t) = W$  is described by the following differential equation:

$$\frac{dz}{dt} = -f'(W)L(t), \quad z(T) = 0 \quad (C1)$$

from which we obtain

$$z(t) = -f'(W) \int_t^T L(x) dx \quad (C2)$$

To calculate  $z(i)$  – that is,  $z$  at the beginning of season  $i + 1$  – we need to calculate the integral on the right-hand side, which is the sum of the integrals for the seasons beginning at  $i, i + 1, \dots, T - 1$ :

$$z(i) = f'(W) \sum_{k=1}^{T-1} e^{-kq_r V} \int_k^{k+S} e^{-q_s t} dt \quad (C3)$$

(we assume that the time unit and the length of the year  $S + V$  coincide) or

$$z(i) = f'(W) \frac{1 - e^{-q_s S}}{q_s} \sum_{k=1}^{T-1} e^{-k(q_s S + q_r V)} \quad (C4)$$

Calculating the sum using the formula for the geometric progression with  $T$  tending to infinity, we obtain the following formula for  $z(i)$  valid for unlimited life span:

$$z(i) = f'(w_\infty) \frac{(1 - e^{-q_s S}) e^{-i(q_s S + q_r V)}}{q_s (1 - e^{-(q_s S + q_r V)})} \quad (C5)$$

We see that  $z(i)$  now does not depend on maximum life span but only on  $i$ . Taking into account that survival at  $t = i$  is equal to

$$L(i) = e^{-i(q_s S + q_r V)}$$

and that

$$z(i) = L(i)$$

at the points of the switching curve, we obtain the expression

$$f'(w_\infty) = \frac{q_s (1 - e^{-(q_s S + q_r V)})}{(1 - e^{-q_s S})} \quad (C6)$$

For the case in which the production rate is given by expression (14), we obtain the following formula for the limiting size:

$$w_\infty^{1-b} = \frac{ab(1 - e^{-q_s S})}{q_s (1 - e^{-(q_s S + q_r V)})} \quad (C7)$$