

# Life history invariants, age at maturity and the ferox trout

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## Summary

Data on brown trout in Norway and on Arctic char in Norway, Iceland, Greenland or Canada are used to make three points about life-history invariants. First, invariants constructed from adaptive programmes of development that are conditioned on growth and mortality rates are more complicated than those constructed solely on the basis of dimensional analysis, but are more consistent with the data. Second, if one allows the possibility of escaping a size ceiling (e.g. by switching from planktivory to piscivory) 'ferox trout' – brown trout that are exceptionally large and long lived – are predicted with the theory only if mortality is size dependent and the growth rate on food sources with different asymptotic sizes differs. Third, a successful empirical approach for finding life-history invariants can be more fully understood as the result of adaptive programmes of development.

**Keywords:** brown trout (*Salmo trutta*); Arctic char (*Salvelinus alpinus*); life history; optimality; ferox trout

## Introduction

To a large extent, biology is the study of variation because a 'specific characteristic of biology is variation; biology which ignores variation is inherently defective' (Berry, 1989). On the other hand, some of the greatest biologists, including Julian Huxley (1932, 1993) and D'Arcy Thompson (1959), sought constancy in the enormous diversity. For example, when one constructs allometric relationships of the form  $Y = AX^b$  (where  $Y$  is a dependent quantity such as metabolic rate,  $A$  and  $b$  are constants and  $X$  an independent quantity such as mass) by comparisons across species (e.g. Calder, 1984), a natural 'invariant' arises because  $Y/X^b$  is constant. Thus, the use of invariants is an attempt to find overarching constancy in variation. Invariants have a long and rich history in applied mathematics (Stahl, 1962; Lin and Segel, 1974), have appeared in ecology in the species–area relationship (Preston, 1960) and food webs (Briand and Cohen, 1984) and have recently been used in evolutionary and behavioural ecology (Charnov and Berrigan, 1990; Charnov, 1991; Mangel, 1992; Charnov, 1993 and references therein; Stephens and Dunbar, 1993; Charnov and Parker, 1995).

In particular, Charnov and colleagues introduced invariants, particularly dimensionless invariants, for the study of life history evolution, building on earlier work by Beverton and Holt (1959). Charnov's (1993) book discusses applications in many areas of evolutionary ecology including sex allocation, ageing, alternative life histories and determinate/indeterminate growth.

Similarly, there are two broad modes of study. One can begin a study with pattern and infer process from the pattern. Alternatively, one can begin with process and predict pattern. That is, one can discover invariants in the data and then seek explanations of the pattern or predict invariants on the basis of a theory and then seek them in the data. Each approach is complementary of the other and valuable to the overall understanding of nature.

In demographic studies of fish populations, modern use of life history invariants began with the work of Alm (1959) and Beverton and Holt (1959). They were motivated by practical problems

in fisheries management (Beverton, 1961, 1987, 1992; Pauly, 1980), particularly in trying to relate the instantaneous mortality rate  $M$  (which is hard to measure) and the rate  $K$  at which asymptotic size is approached (which I shall call the growth rate and which is much easier to measure) because the level of fishing mortality is often set relative to natural mortality. One can consider quantities that have the same units, such as  $K$  and  $M$  or the reciprocal of the age of maturity  $T_m$  and seek combinations that are dimensionless, such as  $K/M$ ,  $KT_m$  or  $MT_m$ . Then, for example, if there is a consistency of  $K/M$ , we can calibrate the value for one stock and use it to estimate mortality, from growth rates, of other stocks. Life-history invariants may also provide information about the evolutionary biology of the organisms (Beverton, 1992; Charnov, 1993).

Following the lead of Charnov and Berrigan (1990) and Charnov (1991, 1993), Vollestad *et al.* (1993) and Vollestad and L'Abée-Lund (1994) studied the quantities  $K/M$ ,  $KT_m$  or  $MT_m$  for the brown trout *Salmo trutta* and the Arctic char *Salvelinus alpinus*, respectively. For the trout, they found that neither  $K/M$  nor  $MT_m$  was constant, while for the char they found that  $MT_m$  was approximately constant but  $K/M$  was not. They were unable to resolve why this is so and proposed that the solution lies in the collection of more data across a large number of species and taxonomic groups (Vollestad *et al.*, 1993). They also discovered that the relative size at maturity (size at maturity divided by asymptotic size) was not constant for trout but increased with increasing asymptotic size and was approximately constant for char.

In the course of developing an explanation for these results, we shall also understand something about a rare form of the brown trout, the ferox trout (Campbell, 1979), which is exceptionally large and exceptionally long-lived.

### The data sources

*A priori*, there is no reason to separate the trout and char data. Insofar as it is based on generic variables, for a theory of invariance to be robust, it should operate over closely related species. Consequently, to simplify the presentation, I combine the two data sets. However, I have run the various analyses separately and will report the separate results in captions of the appropriate figures.

Vollestad *et al.* (1993) give usable data on 28 stocks of brown trout in Norway and Vollestad and L'Abée-Lund (1994) give usable data on 26 stocks of Arctic char in Norway, Iceland, Greenland or Canada. Usable means that the data include the mean or 50th percentile values of asymptotic length  $L_\infty$  (mm), which are obtained by fitting a specified functional form to the growth versus time data, rate of growth  $K$  (per year), rate of mortality  $M$  (per year); age at maturity  $T_m$  (year), defined to be the age at which 50% of the individuals are mature and size  $L_m$  (mm) at maturity. Variances were not given. Three potential invariants are the dimensionless quantities

$$K/M \sim \text{constant} \quad (1)$$

and

$$T_m M \sim \text{constant or } T_m K \sim \text{constant} \quad (2)$$

If Equation 1 were true, then a plot of  $K/M$  versus  $K$  should yield a straight line with zero slope, even though  $K$  appears in the ordinate and abscissa. Similarly, if Equation 2 were true, then a plot of  $T_m M$  versus  $M$  or  $T_m K$  versus  $K$  should yield a straight line with zero slope. However, as Vollestad *et al.* (1993, Figure 2) noted, none of these obtains (Figs 1a, b and 2a). Furthermore, even if Equation 1 or 2 were true, we have no way of predicting the value of the constant *a priori*. On the other hand, the invariant computed using the method described in this paper is both

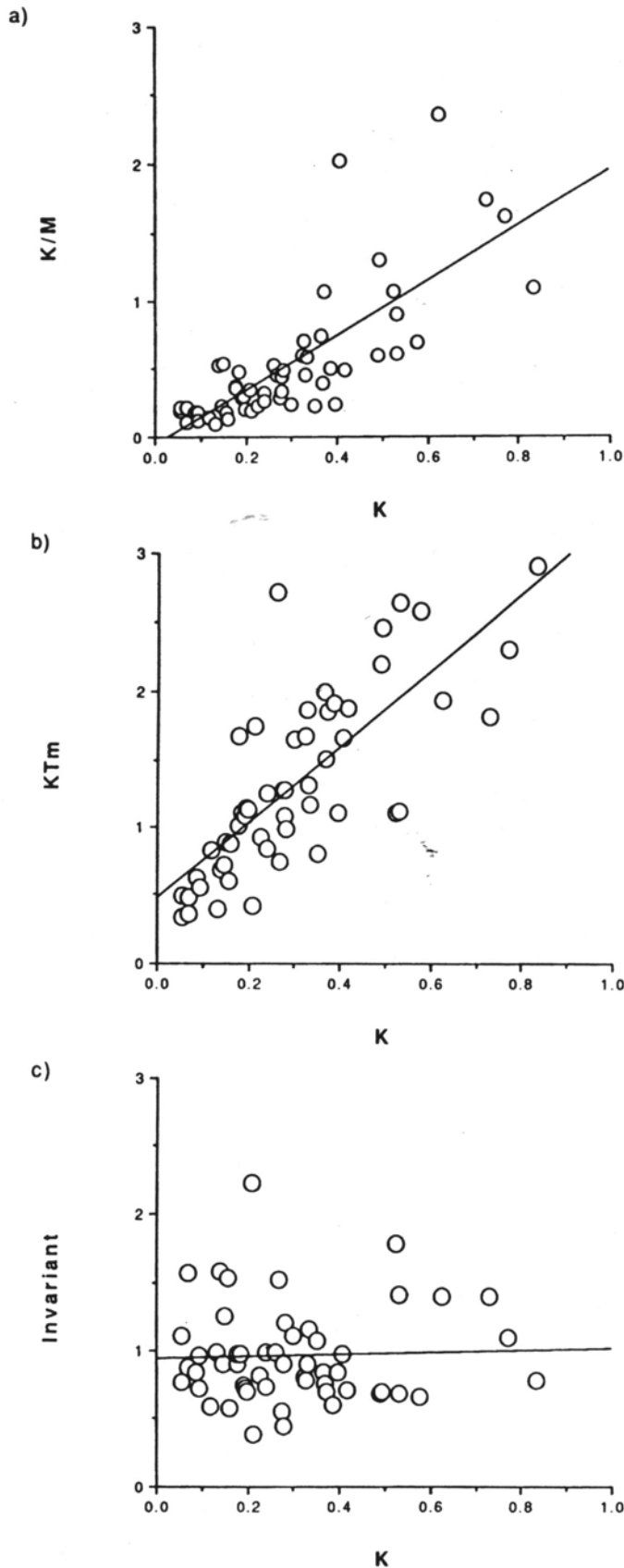


Figure 1. Potential invariants for the trout and char stocks studied in this paper. (a) The quantity  $K/M$  as a function of  $K$  shows a positive slope. The regression line is  $y = -0.058 + 2.00x$  ( $p < 10^{-4}$  for the hypothesis that the slope is 0). When trout and char stocks are separated for the analysis, both show positive slopes with  $p < 10^{-5}$ . (b) The quantity  $KT_m$  also has a positive slope, with regression line  $y = 0.465 + 2.80x$  ( $p < 10^{-4}$ ). When trout and char stocks are separated for the analysis, both show positive slopes with  $p < 10^{-4}$ . (c) The proposed invariant constructed by the use of the methods of this paper is virtually independent of  $K$ . The regression line is  $y = 0.938 + 0.076x$  ( $p > 0.8$ ); the theoretical value should be 1 and independent of  $x$ . When trout and char stocks are separated, the relationship between the proposed invariant and  $K$  has a slightly positive slope and  $p > 0.12$  for trout and a slightly negative slope and  $p > 0.15$  for char.

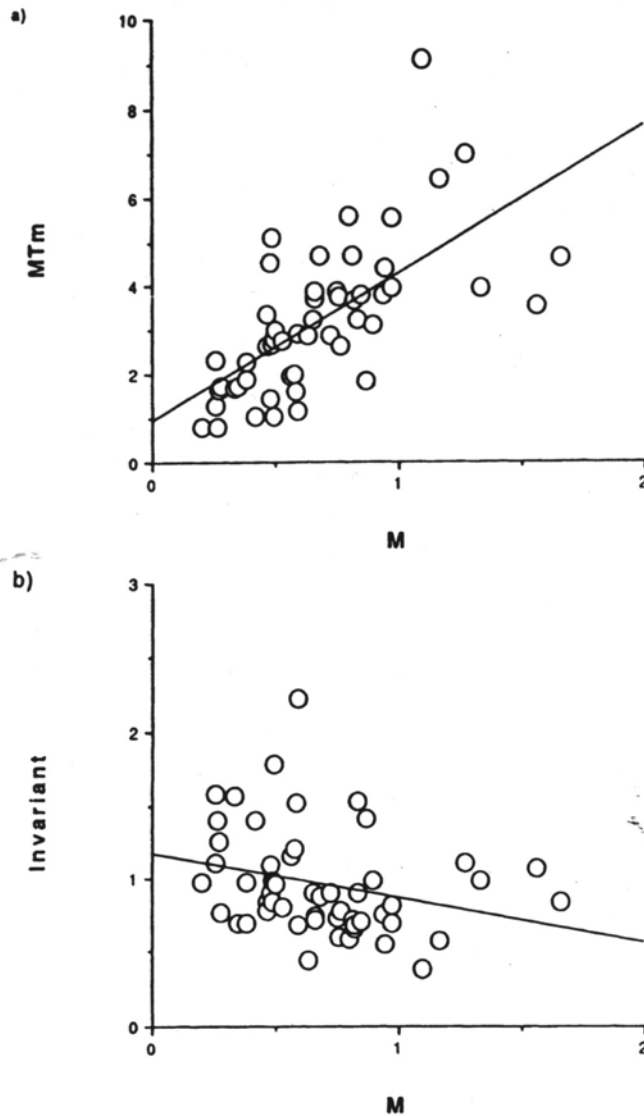


Figure 2. (a) The quantity  $MT_m$  as a function of  $M$  also has a positive slope. The regression line is  $y = 0.929 + 3.35x$  ( $p < 10^{-4}$ ). When trout and char stocks are separated, both slopes are still positive and  $p < 2 \times 10^{-3}$  for each. (b) The proposed invariant constructed by the use of the methods of this paper depends modestly upon  $M$  with regression line  $y = 1.17 - 0.301x$  ( $p > 0.09$ ). When trout and char stocks are separated, both slopes are negative and  $p > 0.075$  for trout and  $p > 0.5$  for char.

predictive (that is, given a value of  $K$  and  $M$ , a particular value of the constant is derived) and much more constant (Figs 1c and 2b).

### The theory

I assume that the rates of growth and mortality are fixed by the genetics and physiology of the fish and the ecological setting of the environment. From these, we can estimate the expected reproductive success for maturity at a given age. Consequently, it is possible to find the optimal

age of maturity, which is an important landmark in the life-history landscape (Mangel and Ludwig, 1992; Roff, 1992; Stearns, 1992).

To begin, assume that length  $L(t)$  at time  $t$  follows the von Bertalanffy (1957) growth formula

$$L(t) = L_{\infty}(1 - e^{-K(t-t_0)}) \quad (3)$$

where  $t$  is time measured in years and  $L_{\infty}$  is the asymptotic length. The parameter  $t_0$  is included to take account of the differences in the early life-history (egg and larvae) growth patterns and later ones, to which the growth curve is usually fitted (Wootton, 1990; Kamler, 1992). If mortality  $M$  is assumed to be constant across body sizes, survival to time  $t$  is  $e^{-Mt}$ .

Assuming that the weight is proportional to the length cubed and that the reproductive success is proportional to the weight, the definition of fitness is

$$F(t) = e^{-Mt}[L_{\infty}(1 - e^{-K(t-t_0)})]^3 \quad (4)$$

Setting  $c = \exp(Kt_0)$ , the optimal age at maturity is

$$t^* = \frac{1}{K} \log\left(\frac{Mc + 3Kc}{M}\right) \quad (5)$$

The first prediction of this relatively simple theory is that age at maturity is independent of asymptotic size (Fig. 3), which does not seem to be the case for the trout and char data. The reason for this difference will be explained below. The second prediction is that  $t^*K$  and  $t^*M$  are inherently non-linear functions of growth and mortality rates. That is, we should not expect them to be invariant. If  $t_0 = 0$ , then  $c = 1$  and from Equation 5

$$t^*K = \log\left(\frac{M + 3K}{M}\right) = \log\left(1 + \frac{3K}{M}\right) \quad (6)$$

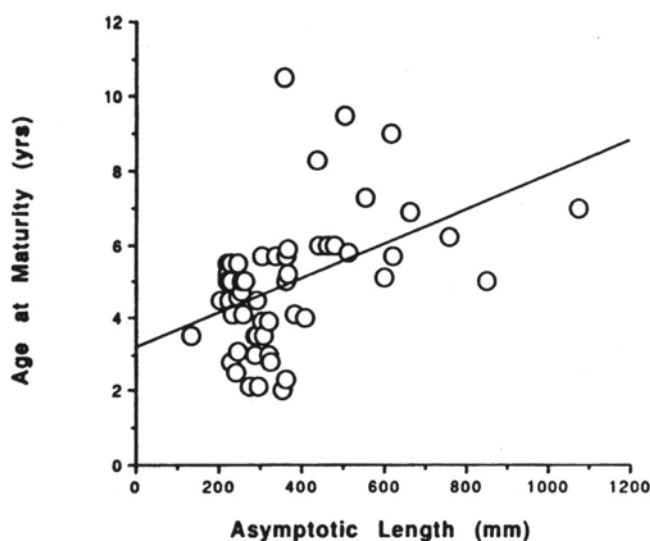


Figure 3. The relationship between age at maturity and asymptotic length. The simple optimality theory predicts that age at maturity should be independent of asymptotic length, which is a fitted (versus biological), parameter. The regression line is  $T_m = 2.47 + 0.0046 L_{\infty}$  ( $p < 0.01$ ).

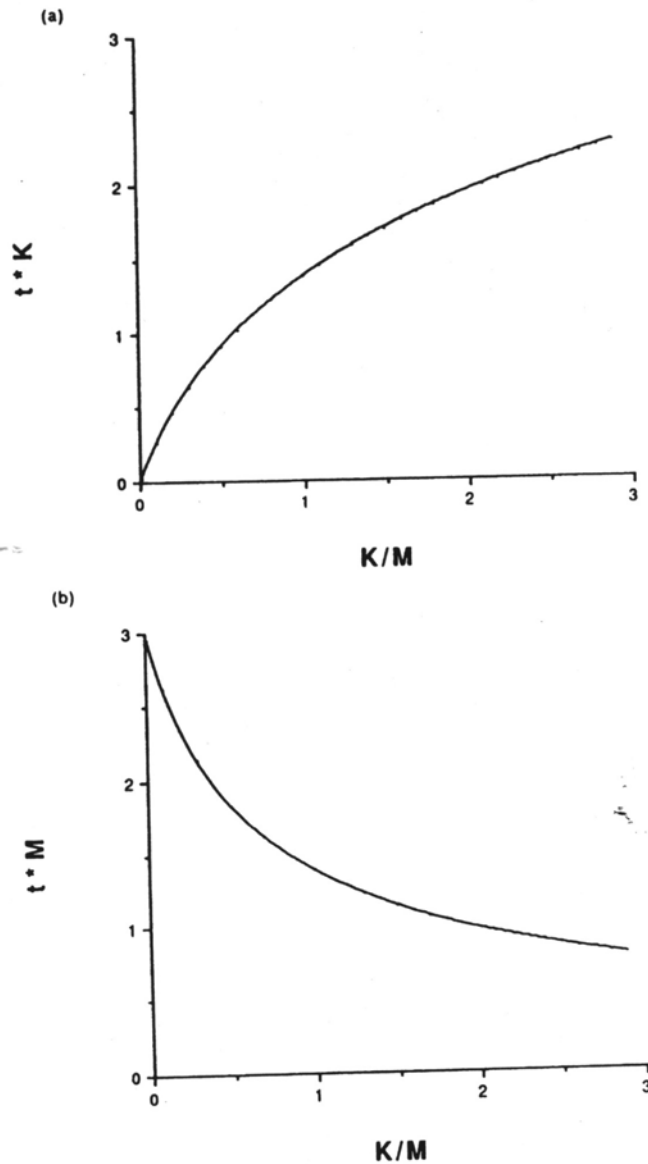


Figure 4. When  $t_0 = 0$ ,  $t^*K$  and  $t^*M$  are functions of  $K/M$  only, but in both cases are highly non-linear functions of that ratio.

which depends only upon the ratio  $K/M$  but in a highly non-linear way (Fig. 4a). If  $K/M$  is small, since  $\log(1+x) \sim x$ ,  $t^*K \sim 3 K/M$ . Similarly,

$$t^*M = \frac{M}{K} \log\left(1 + 3\frac{K}{M}\right) \quad (7)$$

also only depends upon the ratio  $K/M$  but again in a highly non-linear fashion (Fig. 4b). These results are applicable only if  $t_0 = 0$ .

The predicted age at maturity accords well with the data (Fig. 5). Roff (1991) did a similar computation in which  $t_0 = 0$  (his Equation 5 and Figure 2) for flatfishes. The agreement in that

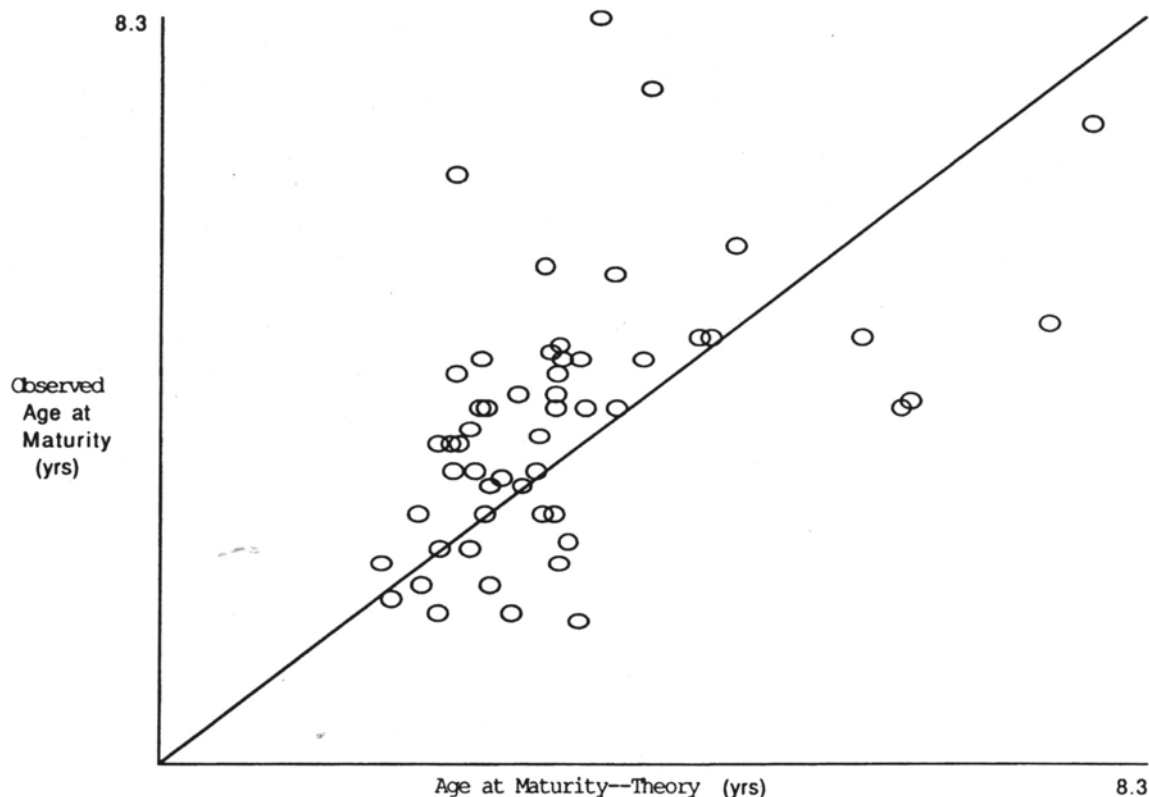


Figure 5. The theory given by Equation 5 is consistent with the data ( $p > 0.75$ ). The mean deviation between the theory and the observations is  $-0.077$  year. I have used  $t_0 = 1$  in the calculation. Repeating the calculation in which  $t_0 = 0$  (so that  $c = 1$ ) gives a mean deviation nearly twice as large ( $-0.123$ ) and  $p < 0.01$ . However, I did not attempt to find the value of  $t_0$  that gives the best fit to the data.

case between the predicted and observed age at maturity is also excellent. Thus, intraspecific variation in age at maturity may result from adaptive programme of maturation. This type of analysis also has important implications for management, as first noted by Sidney Holt in 1958 (Beverton, 1992, p. 141).

Equation (5) can be used to construct an invariant. That is from Equation 5, we predict that

$$T_m K / \log\left(\frac{Mc + 3Kc}{M}\right)$$

is invariant and should equal 1. Note that this quantity involves all three parameters  $T_m$ ,  $K$  and  $M$ . The invariant constructed in this manner does not depend strongly on either  $M$  or  $K$  (Figs 1c and 2b). From the applied perspective, Equation (5) can be viewed as an equation that determines  $M$ , given  $K$  and  $T_m$ , so that we could infer natural mortality from measurements of growth rate and age at maturity. Beverton (1992) reaches a similar invariant in a different manner.

Next consider relative size at maturity,  $L_m/L_\infty$ . Following Roff (1991) and Beverton (1992), we substitute Equation 5 into Equation 3 to find

$$\frac{L_m}{L_\infty} = 1 - \frac{M}{M + 3K} = \frac{3K}{3K + M} \quad (8)$$

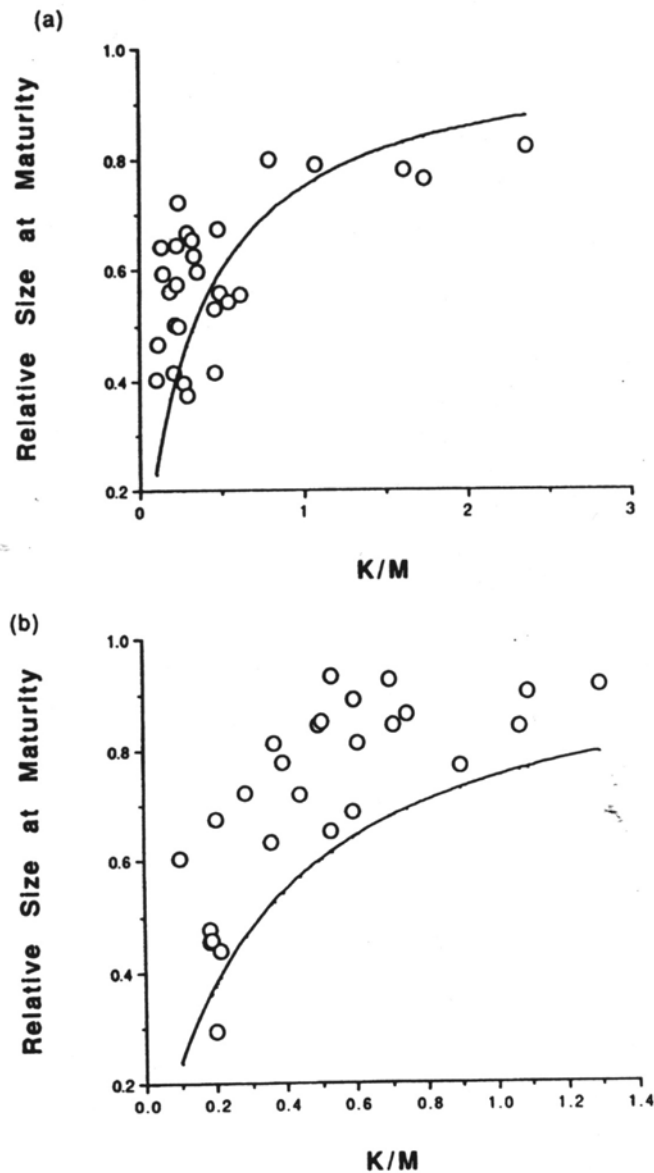


Figure 6. The relative size at maturity predicted by Equation 8 is (a) accurate for trout, but (b) underestimates the relative size at maturity for char.

regardless of the value of  $t_0$ . Note that the relative size at maturity will only be a function of  $K/M$ . This prediction works well for trout (Fig. 6a) but not so for char (Fig. 6b). The reason for the latter is unknown. Equation 8 suggests another potential invariant. We predict that

$$\frac{L_m}{L_\infty} / \frac{3K}{3K + M}$$

will be invariant (and equal to 1). This suggests that adaptive programmes of development may indeed be an invariant of life history.



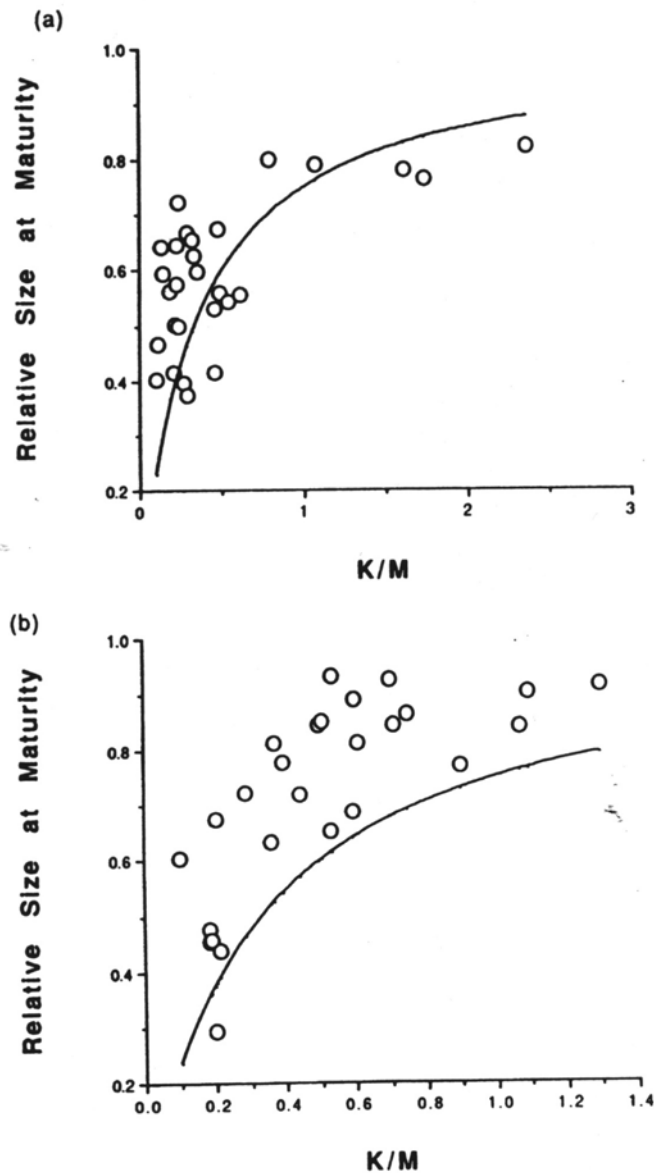


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The problem remains that age at maturity is predicted to be independent of asymptotic length, but this appears not to be the case. The source of the difficulty is the way that the asymptotic length enters into fitness in Equation 4. When the optimal age at maturity is computed, asymptotic length factors out of the computation. An alternative growth model is that of Richards (1959)

$$L(t)^s = L_{\infty}^s - [L_{\infty}^s - L_0^s]e^{-Kt} \quad (9)$$

where  $s$  is a 'shape' parameter and  $L_0$  is initial size (i.e.  $L(0) = L_0$ ). Setting  $s = 1$  gives an expression analogous to Equation 1:

$$L(t) = L_{\infty} - [L_{\infty} - L_0]e^{-Kt} \quad (10)$$

The optimal age at maturity associated with Equation (10) is

$$t^* = \frac{1}{K} \log\left(\left(\frac{M+3K}{M}\right)\left(\frac{L_{\infty}-L_0}{L_{\infty}}\right)\right) = \frac{1}{K} \log\left(\left(\frac{M+3K}{M}\right)\left(1 - \frac{L_0}{L_{\infty}}\right)\right) \quad (11)$$

In this case,  $t^*$  depends upon the ratio of initial and asymptotic size and  $\partial t^*/\partial L_{\infty} > 0$ , so that age at maturity increases with asymptotic size.

If one wanted to simply fit growth data to a model, then clearly either Equation (3) or (6) would be suitable and once the parameters were estimated, the quality of the fit between the data and growth curve would be identical. The same is not true, however, if one wants to make evolutionary predictions. Great care must be taken to understand the hidden assumptions in such models if one is to use them for evolutionary analyses (e.g. Georgiadis, 1985).

### The ferox trout: escaping the ceiling

The reanalysis of the data on trout and char provides a framework for understanding a remarkable form of brown trout. In some Scottish and Irish lakes, there are populations of very large (up to 100 cm) and very old (up to 15 years) brown trout called ferox trout. The ferox trout are reviewed in Elliott (1994, pp. 132–133) and Finch (1990, pp. 142–3), who noted that we lack age-related mortality information. Campbell (1979) suggests that these individuals are exceptional because they crossed a critical threshold and then were able to eat Arctic char, *S. alpinus* (L.). That is, an individual may be able to escape a size ceiling (determined by its ontogeny and the kind of food) and ultimately reach a much larger ceiling. A similar situation occurs for perch (*Perca fluviatilis* L.) in Lake Windermere (Le Cren, 1992) where the big perch (400 versus 180 mm) were predominantly piscivorous. Elsewhere, Ilina (1973) found that the progeny of a single pair of perch formed three separate ecological groups, with the largest group feeding on fish fry.

One of the best-studied cases (Ferguson and Mason, 1981; Hamilton *et al.* 1989; Ferguson and Taggart, 1991) is the trout in Lough Melvin, Ireland. Four morphotypes and life histories are identified there.

(1) Ferox trout are dull brown or green with little or no spotting. Their heads are disproportionately long with a wide mouth and many large teeth. They are chiefly piscivorous (eating trout, perch and char) after the age of 3 years and can live to very old ages (> 12 years). They spawn in the deep downstream section of largest inflowing river.

(2) Sonaghen trout are dark or silvery with many large black spots. Red spots, if present, are restricted to the posterior part of the body. They have dark or black fins, with elongated pectorals. They chiefly feed in midwater on invertebrates and rarely live past 5 years. They spawn in smaller inflowing rivers.

(3) Gillaroo trout are golden brown or yellow with many large orange-red spots, especially below the lateral line. Their head is small in proportion to a deep compressed body. They feed almost exclusively on benthic invertebrates and rarely live past 5 years. They spawn in the lake and outflowing river.

(4) Brown trout are all trout not fitting into any of these three categories.

Ferguson and colleagues, using *Ldh-5* as a phylogeographic marker locus, proposed that the ferox trout is the ancestral form, that these three forms are reproductively isolated and that they should be treated as races for purposes of conservation.

A full analysis of the ferox trout must capture the ontogeny of the fish, the transition to piscivory and habitat selection (e.g. Juanes, 1994; Juanes *et al.* 1994). Consequently, it requires a dynamic, state-variable model (Mangel and Clark, 1988; Mangel and Ludwig, 1992) that is beyond the scope of this paper. For example, there is evidence in largemouth bass (Applegate and Kruckenberg, 1978; Wickler and Johnson, 1987) that a shift to piscivory from planktivory requires that the fish achieve a critical size within a certain interval if they are to be effective predators of other fish and this requires an appropriate pattern of plankton when the fish are younger and smaller. Although forage fish may not be essential for survival, they may be for achieving large size. Ovsyannikov (1992, 1993) has started the development of a theory that may point in this direction. Such a full analysis involves a major shift in perspective since, to date, most studies of life-history invariants have focused on the population or species level whereas the shift to piscivory is clearly an individual phenomenon.

Rather than a full analysis, here I provide a brief retrospective treatment of the ferox trout, in order to make two points about it. To capture the idea of escaping a size ceiling, suppose that there are two possible asymptotic lengths,  $L_1$  and  $L_2$ , in which  $L_1 \leq L_2$ , two associated growth rates,  $K_1$  and  $K_2$  and a mortality rate  $M$  that is independent of size but that there is only a chance  $p$  that the fish's genetics and physiology and the environment are conducive to the larger asymptotic size. In such a case, we replace Equation 4 by

$$F(t) = e^{-Mt} \{ p[L_1(1 - \exp(-K_1(t-t_0)))^3] + (1-p)[L_2(1 - \exp(-K_2(t-t_0)))^3] \} \quad (12)$$

The optimal age at maturity cannot be obtained analytically from Equation 12. Comparing Equations 4 and 12, one sees that if the two growth rates are the same, the age of maturity will be the same, even if the asymptotic sizes are very different. That is, we predict the existence of ferox trout only if  $K_2$  differs from  $K_1$ . Numerically exploring the predictions of Equation 12, allowing  $p$  and the ratio  $L_2/L_1$  to vary and examining the length and age at maturity leads to the discovery that although Equation 12 leads to potentially large fish, it does not lead to extremely old fish. To obtain such a prediction, one must modify Equation 12 to allow size-dependent mortality. If the mortality rate decreases as size increases, which is generally true (McGurk, 1986), then we predict fish that are both large and old. The introduction of size-dependent mortality adds biological realism (Peterson and Wroblewski, 1984; McGurk, 1986) even if it complicates the analysis. Recent work by P. Abrams and L. Rowe (personal communication), however, shows that size-independent mortality may not necessarily lead to simple predictions when it is coupled with other aspects of life history. In summary, the methods used in this paper predict ferox trout only if the growth rates for the two asymptotic sizes differ and if there is size-dependent mortality. Both of these are empirically testable. A similar conclusion was drawn by Barry and Tegner (1990) in their attempt to construct bimodal size distributions for populations of sea urchins.

### Empirical methods for finding life-history invariants

Empirically determined invariants date at least to Kepler (Langley *et al.*, 1987), who may have discovered the laws of planetary motions by manipulation of the data until invariants were obtained (Langley *et al.*, 1987). One of the methods advocated by Charnov (1993) is essentially an empirical approach. In this method, one plots the mean adult lifespan, approximated by  $1/M$  (Hoenig, 1983), against the age at maturity and forces a regression line through the origin. If this line has a constant slope, then

$$\frac{1}{\bar{M}} = \frac{1}{MT_m}$$

is constant, so that  $MT^m$  is an invariant. This reasoning motivated the work of Vollestad and colleagues discussed earlier.

Here, I illustrate how Monte Carlo simulation can be used to illuminate the success of the empirical method. As before, assume that the growth rate and mortality are fixed and that the age at maturity evolves in response to these quantities (Beverton, 1961, 1987, 1992; Pauly, 1980; Mangel, 1994; Nonacs *et al.* 1994). Then, the fitness is given by Equation 4 and the optimal age at maturity by Equation 5.

To mimic the empirical approach, assume that  $K$  and  $M$  vary across populations;  $\log(K)$  is normally distributed with mean  $m_k = 0.5$  and standard deviation  $\sigma_k = 0.3$  and  $\log(M)$  is normally distributed with mean  $m_m = 0.5$  and standard deviation  $\sigma_m = 0.3$ . Each pair  $\{K, M\}$  leads to the optimal age at maturity determined by Equation 5 and the fitness associated with that age at maturity by Equation 4; I used  $t_0 = 0$  for computations. One draws a large number of pairs  $(K, M)$ , computes the optimal age at maturity, plots the life span ( $= 1/M$ ) as a function of the age at maturity and fits a linear regression through the origin and the points  $(T_m, 1/M)$ . The results (e.g. Fig. 7) are remarkably similar to those presented by Charnov (1993). Thus, it appears

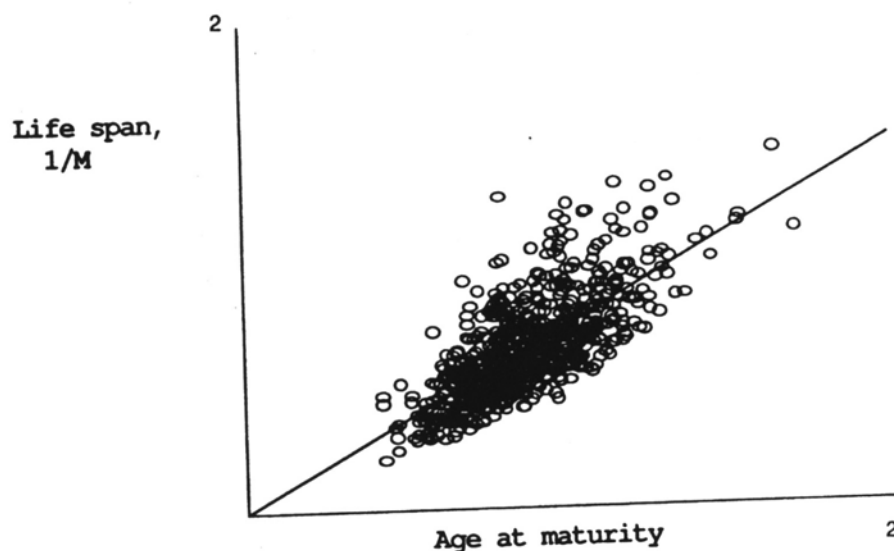


Figure 7. The relationship between life span, defined to be  $1/M$  and age at maturity, computed from Equation 5, for 800 randomly drawn values of  $K$  and  $M$  in which  $\log(K)$  and  $\log(M)$  are normally distributed. The regression line through the origin has a slope similar to that reported by Charnov (1993).

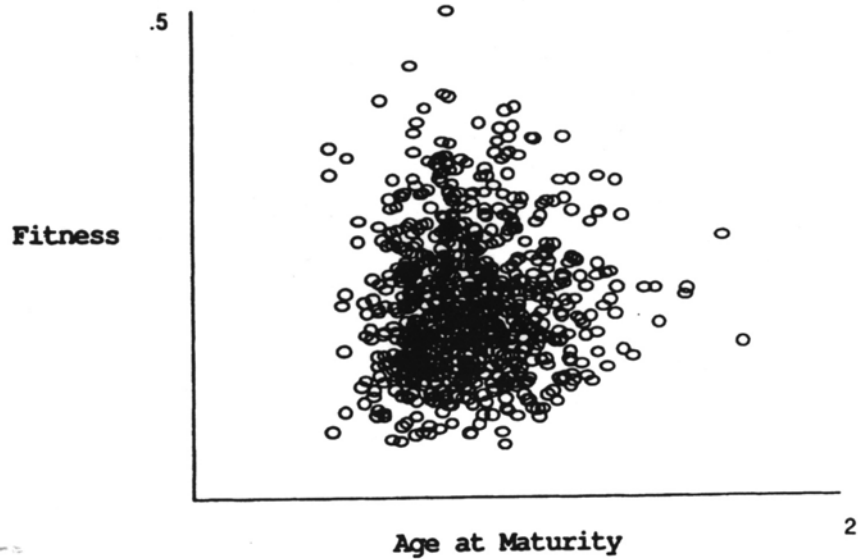


Figure 8. The fitness for the same 800 points as in Fig. 7 as a function of age at maturity. Note that there is little or no dependence of fitness on age at maturity.

that there is indeed constancy to product  $T_m M$ ; part of the reason for this discovery is the use of a large number of pairs of values and forcing the regression line through the origin. Were Fig. 7 all that we had, it would not be possible to understand the origin of this constancy. The general pattern in Fig. 7 is maintained with different choices for the distribution of the parameters.

However, in this case, we know exactly the adaptive relationship between age at maturity and  $1/M$ . Furthermore, the fitness associated with different pairs  $(K, M)$  shows no particular trend with age at maturity (Fig. 8). That is, the role of development (maturity), in this case, is to modulate the interplay of growth and mortality so that individuals facing different growth and mortality conditions do approximately equally well in terms of expected reproduction. We are thus able to obtain a better understanding of why the empirical approach leads to apparent invariants.

### Discussion

Giske *et al.* (1993) proposed that a better phenotypic measure for the determination of life histories is

$$\frac{\log(R_0(t))}{t} - r$$

where  $R_0(t)$  is the expected reproductive success when age at maturity is  $t$  and  $r$  is the rate of growth of the population. As they noted, when the mortality rate is constant across size and age, the optimal age at maturity does not depend at all on  $M$ , which is problematic. In that case, the optimal age at maturity is the oldest one possible. On the other hand, for organisms with discrete generations, a more appropriate measure of reproductive rate might be

$$\frac{R_0(t)}{t} - r$$

Keeping constant mortality, the quantity to maximize is now  $F(t)$ , which is determined by Equation 4, divided by  $t$ . This quantity has an internal maximum (i.e. neither 0 nor infinity) for the values of  $K$  and  $M$  used here. However, the condition for determining the age at maturity is sufficiently complicated that no analytical solution could be found and, consequently, one cannot compute an invariant analogous to the one based on Equation 5.

Furthermore, the age at maturity based on  $F(t)/t$ , rather than  $F(t)$  is a poorer predictor of the observed age at maturity. For example, the sum of the squared deviations between the prediction, Equation 5, and the observed data is approximately 179, whereas the sum of the squared deviations between the predicted age of maturity based on  $F(t)/t$  and the observed data is approximately 450. The rate-based predictor consistently underestimates the observed age at maturity.

The simplest invariants, which are constructed only on the basis of dimensional considerations, are very appealing on considerations of elegance. In addition, the combination  $K/M$  (or its reciprocal) has a basis in theoretical behavioural ecology as a rule for life-history evolution (the 'minimize  $\mu/g$ ' rule, where  $\mu$  is the mortality rate and  $g$  is the growth rate; Gilliam and Fraser, 1987; Mangel and Ludwig, 1992), making it even more appealing. However, the results from my analysis suggest that more complicated invariants derived from the life-history considerations may actually provide more insight into the interaction of the relevant biological variables.

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