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Abstract

We revisit the empirical equation of Gislason *et al.* (2010, *Fish and Fisheries* **11**:149–158) for predicting natural mortality (M, year^{-1}) of marine fish. We show it to be equivalent to $M = \left[\frac{L}{L_\infty}\right]^{-1.5} \cdot K$, where L_∞ (cm) and K (year^{-1}) are the von Bertalanffy growth equation (VBGE) parameters, and L (cm) is fish length along the growth trajectory within the species. We then interpret K in terms of the VBGE in mass $\left(\frac{\mathrm{d}W}{\mathrm{d}T}\right)$, and show that the previous equation is itself equivalent to a −⅓ power function rule between M and the mass at first reproduction (W_α); this new −⅓ power function emerges directly from the life history that maximizes Darwinian fitness in non-growing populations. We merge this M, W_α power function with other power functions to produce general across-species scaling rules for yearly reproductive allocation, reproductive effort and age at first reproduction in fish. We then suggest a new way to classify habitats (or lifestyles) as to the life histories they should contain, and we contrast our scheme with the widely used Winemiller–Rose fish lifestyle classification.

Keywords fish growth, natural mortality, optimal life history

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Introduction: what are assembly rules for fish life histories?

This study addresses life histories in female fish; what we call 'assembly rules for fish life histories' refers to the relationships between mortality rate, an individual's growth (production) rate, size (age) at first reproduction, reproductive allocation thereafter and egg size. Natural selection mediates these relationships and favours some very special ones (Winemiller and Rose 1992; Charnov 1993). These special ones are what we aim to predict, hence our use of the term 'evolutionary'. As a life history consists basically of a creature surviving and growing to the optimal size to start offspring production, we concentrate on the size (age) of first reproduction. Most fish species have indeterminate growth, where body size still increases after initiation of reproduction/maturity. We will approximate fish growth and reproduction with a 'determinate growth approximation,' where growth ceases at the onset of adulthood. This approximation captures the essential power function forms we wish to study, even though the normalization constants generally differ between determinate and indeterminate growth.

Our evolutionary optimization scheme yields relationships that are applicable across species between mortality, individual growth rate, body size (age) at maturity and reproductive effort (Charnov 1993). The scheme suggests how we should classify habitats with respect to what life histories they will contain, and we end up proposing a new way to classify the interaction of habitat (or lifestyles) and life history. We will contrast this to the widely used Winemiller–Rose classification scheme, a variant of 'r/k' selection theory.

Surprisingly, the size of an individual offspring (egg size) is decoupled from the previous evolutionary optimization, and we can only provide hints as to what sets optimal egg size (Smith and Fretwell 1974). Luckily, this decoupling means that we need not solve the optimal egg size problem to predict the optimal size at maturity. This decoupling happens because we use R_0, the net reproductive rate, as an individual's fitness measure (Charnov 1993, 1997; see also Appendix 2) and because we place all density dependence among the very young (the standard kind of spawner/recruit assumption in commonly used fishery models).

Introduction to natural mortality: two distinct ways for *M* to be size dependent

Externally imposed mortality plays a key role in the optimal size (age) for the initiation of reproduction, so first we study natural mortality in fish and how it relates to individual body weight and to body weight at maturity both within and across species.

Opinion about the natural mortality (M) of fish is polarized into those who believe M, at least near adulthood, can be treated as an age/size-independent constant within the species (e.g. Beverton and Holt 1957, 1959; Pauly 1980), and those who believe M often is a strong and well-defined negative function of body size, up to and perhaps beyond the length of first reproduction (L_α) (see Gislason *et al.* 2010 for a general overview). Both camps agree that M is very high for larval (and other smaller) fish, but they disagree as to whether M drops and then remains approximately constant well before L_α or whether it shows some well-defined function of length, L_x. Following the lead of Beverton and Holt (1959), Charnov (1979), Pauly (1980), Charnov (1993) and others (e.g. Cury and Pauly 2000; Griffiths and Harrod 2007; Andersen *et al.* 2009) have shown that M near the age of first reproduction (α) shows the across-species rule of $M = C{\cdot}K$, where K is the Bertalanffy growth constant for the species growth curve; a typical C value for fish of ≈1.8. Charnov (1993) showed this rule with $C \approx 1.5$–1.7 in a large sample of indeterminate growing reptiles, snakes and lizards, so the rule appears to apply to other organisms with indeterminate growth, as well; Charnov (1979) showed it for marine shrimp. However, M is also known to decrease with asymptotic length (L_∞) across species (e.g. Cury and Pauly 2000); presumably this M refers to M near adulthood. But these M, L_∞ plots are often quite noisy.

In apparent opposition to this constant M idea, a large amount of fish data demonstrate well-defined M effects of body size, both for factors like predation risk and total M at some L_x (e.g. McGurk 1986; Lorenzen 1996). Indeed, models designed to simulate the body size spectra of marine fish communities (e.g. Andersen and Beyer 2006; Pope *et al.* 2006) predict size-dependent scaling of M during ontogeny.

This literature intermingles two questions/ideas: (i) How does M change with L over a growth curve within a species? Are there general scaling rules $M \propto L^{-P}$?, and (ii) How does M, as some sort of average near adulthood (call it M_α), change with body size (say, L_∞) across species? Clearly, if we know M near maturation size and $M \propto L^{-P}$ at other sizes, we can know M at all sizes. But, why should M_α decline with L_∞ across species?

In this study, we first reconcile the within-species M vs. L with the between-species M_α vs. L_∞ puzzle. We will do this by means of life-history optimization. First, the data.

M vs. *L*, within and between species: the data

In a modelling study of the North Sea fish community, Gislason *et al.* (2008) found that M should scale with both L_∞ and L to generate spawner-for-spawner replacement, corresponding to a net reproductive rate $R_0 \approx 1$, and hence coexistence, for large and small species of fish. They also found that this could explain the strong negative relationship between the maximum slope of the stock-recruitment curve at the origin and L_∞ observed by Denney *et al.* (2002). To test this further, Gislason *et al.* (2010) made a careful and critical review of empirical estimates of natural mortality, M (year^{-1}), in marine (and brackish) water fish species and found that the observations could be fit by the following equation (length in cm):

$$\log_e(M) = 0.55 - 1.61\log_e(L) + 1.44\log_e(L_\infty) + \log_e(K) \quad (r^2 = 0.62, n = 168) \tag{1}$$

The L_∞ and K are from fitting the von Bertalanffy growth equation (VBGE) to size at age (x) data:

$$L = L_\infty(1 - e^{-K\cdot x}) \tag{2}$$

Although Gislason *et al.* (2008) provide a biological justification for the terms of Equation 1, it is seemingly a mystery. In particular, the 1.44 scaling of M with L_∞ seems puzzling as mortality rates are expected to decrease with body mass across species. There is one other puzzle here in that the authors also fit a version of Equation 1 with an added Arrhenius term (d/T_a, where d is a constant, and T_a is absolute temperature) and they expected a negative d coefficient, but the fit showed no significant temperature effect when K was also in the equation.

There are two things to note about this equation. First, the coefficients of $log_e(L)$ and $log_e(L_\infty)$ (1.61 and 1.44, respectively) are not statistically different, so it seems reasonable to fit the M equation with a common exponent. This fit is just as good as Equation 1:

$$\log_e(M) = -0.05 - 1.46\log_e\left(\frac{L}{L_\infty}\right) + \log_e(K) \quad (r^2 = 0.61, n = 168)$$

or, more simply, as the intercept is not different from 0, nor the exponent from 1.5,

$$M = \left(\frac{L}{L_\infty}\right)^{-1.5} \cdot K \tag{3}$$

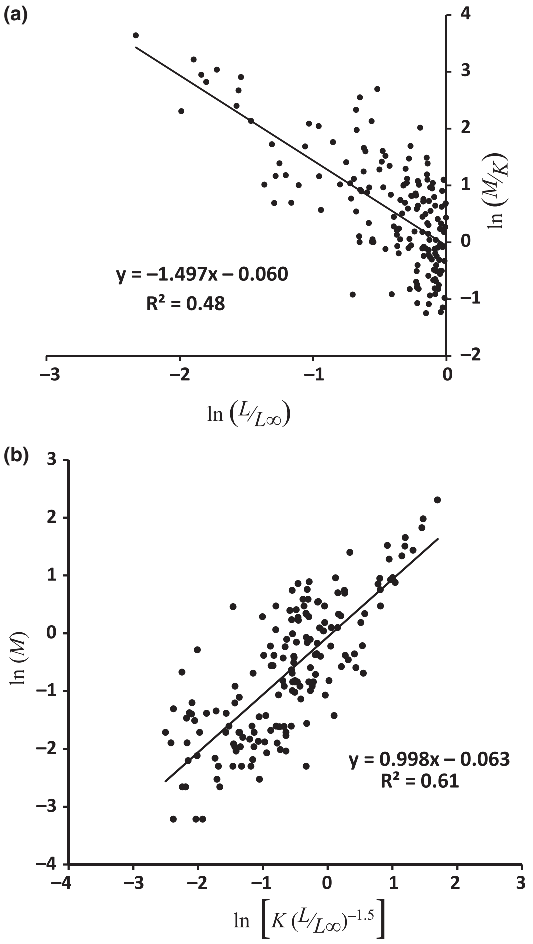

Figure 1 (a) Plot of M/K vs. L/L_∞ in the Gislason *et al.* 2010 data set. See text for discussion. (b) Plot of $\log_e M$ vs. $\log_e\left[K\left(\frac{L}{L_\infty}\right)^{-1.5}\right]$ yields a very useful predictive equation for M; standard error of slope = 0.06 and standard error of intercept = 0.07.

The form of Equation 3 is quite interesting; in Fig. 1a, we show the fitted relation $\log_e\left(\frac{M}{K}\right) = (C_0) + (C_2) \cdot \log_e\left(\frac{L}{L_\infty}\right)$. There is a lot more scatter here ($r^2 = 0.48$, n = 168), but C_0 may be taken as zero ($C_0 = -0.06$; 95% CI: −0.21 to 0.09) and C_2 as −1.5. Surprisingly, the fit is reasonably good down to L/L_∞ values of ~0.15, very small fish, about 20% the size of first reproduction ($L_\alpha/L_\infty \sim 2/3$). So, Equation 3 predicts the M vs. ontogenic L at any fixed K value. We also fit Equation 3 using L/L_∞ data for only the post-maturation period (only $L/L_\infty > 0.65$); this gave the same parameter values as the full L/L_∞ range, so the M, L/L_∞ rule extends into the adult size groups. Finally, we fit the equation with the 60% of the data that came from unfished (or lightly fished) populations, and the answer was again the same.

Second, Equation 1 turned into Equation 3 also predicts the empirically observed M_α vs. K relation across species. Setting ($L/L_\infty \sim 2/3$), the expected relative maturation size, gives ($M_\alpha/K \sim 1.84$), quite typical for indeterminate growers (i.e. fish, lizards, and snakes; see Figs. 4.5 and 4.11, pp. 66 and 74 in Charnov 1993).

So, the Gislason *et al.* 2010 equation supports both the M vs. L (over the life history) position, and the M_α vs. K position. In Fig. 1b, we fit the log/log form of Equation 3, fixing the exponent at −1.5: $\left[\log_e(M)\text{vs.}\log_e\left(K \cdot \left(\frac{L}{L_\infty}\right)^{-1.5}\right)\right]$.

The fit is good ($r^2 = 0.61$), and the residuals here are normally distributed, so this regression should be useful in prediction of M from K, L, L_∞ data.

K is $\propto W_\infty^{-1/3} \propto W_\alpha^{-1/3}$

To understand what Equation 3 means, we must first understand what K is. Fishery scientists usually think of K as the curvature of the growth equation in length (see Equation 2); fish length-at-age data are usually very well described by Equation 2. The production process underlying growth, however, is dW/dt, where W is mass (or more commonly just called weight). $W = a{\cdot}L^3$ for fish that grow isometrically.

The differential equation for the VBGE is as follows:

$$\frac{dW}{dt} = A \cdot W^{2/3} - B \cdot W \tag{4}$$

Solving Equation 4 for $W(x)$ and transforming to $L(x)$ yields Equation 2.

In Appendix 1, we derive several useful properties of this growth/production equation. In particular, we can derive W_∞ (or L_∞) and K from the A and B parameters.

$$K = B/3 \tag{5a}$$

$$W_\infty^{1/3} = A/B = a^{1/3} \cdot L_\infty \tag{5b}$$

and hence that:

$$K = \left(\frac{A}{3}\right) W_\infty^{-1/3} \tag{5c}$$

So, in terms of A and B, we have two ways to answer what K is. First, (Equation 5a) $3 \cdot K \cdot W$ is the term subtracted from a basic production term ($A \cdot W^{2/3}$); Charnov (1993, 2008) has argued that $3 \cdot K \cdot W$ is really mostly a reproductive allocation. Equation 5c, however, shows that K is *also* a −⅓ power function of W_∞. The intuition here is that if K is related to reproductive allocation, *higher K* exhausts the productive capacity ($A \cdot W^{2/3}$) faster, and yields smaller asymptotic size (W_∞). We will work with this power function form of K, using it in two ways. First, we shall write the fitted, empirical Equation 3 in terms of W_∞ (or L_∞). Second, we shall argue that the power function is really about the size at first reproduction (L_α or W_α) and not the asymptotic sizes, because $W_\alpha \propto W_\infty$.

So, using Equation 5c, empirical Equation 3 for M can be written as:

$$M = \left(\frac{W}{W_\infty}\right)^{-1/2} \cdot \left(\frac{A}{3}\right) \cdot W_\infty^{-\frac{1}{3}} \tag{6a}$$

or

$$M = \left(\frac{L}{L_\infty}\right)^{-1.5} \cdot \left(\frac{1}{a^{1/3}}\right) \cdot \left(\frac{A}{3}\right) \cdot L_\infty^{-1}, \tag{6b}$$

Beverton and Holt (1959) first showed that $L_\alpha \propto L_\infty$ within many fish taxa with a central value of ≈⅔. While various taxa differ somewhat (e.g. Clupeidae ≈0.8), ⅔ is widely accepted and used in the fishery literature. It seems less well appreciated that $L_\alpha/L\infty = 2/3$ means that $W_\alpha/W\infty = (2/3)^3 = 0.296$, *the inflection point for the VBGE in mass* (see Appendix 1). When we describe fish growth with equations like the VBGE, our fitting puts the mass at first reproduction (W_α) approximately at the size of the fastest growth. Why? The answer is probably as follows. Although the VBGE well describes fish growth, Equation 4 is somewhat simplistic; the underlying growth process really has two phases: before maturation, fish grow their self; after maturation, they grow slower because production also is given to reproduction. Almost any body mass power function for growth has dW/dt increasing with W at small W. Thus, if the growth rate decreases because of the initiation of allocation to reproduction (size L_α, W_α), the fastest growth – highest dW/dt – will just be at that size. If we fit a VBGE to fish data, we will be putting L_α near the highest dW/dt. And, the inflection point – the highest dW/dt in the VBGE – is at $0.296 \cdot W_\infty$, or $L_\alpha = 2/3 \cdot L_\infty$.

Using these two rules allows us to write Equation 6 in terms of W_α or L_α, the size at first reproduction. Substituting $W_\alpha/(0.296)$ for W_∞ in Equation 6a yields:

$$M = 0.41\left(\frac{W}{W_\alpha}\right)^{-1/2} \cdot A \cdot W_\alpha^{-1/3} \qquad (7)$$

Body size (W_α) at first reproduction

Equation 7 is the most basic equation of all; set $W = W_\alpha$, then:

$$M_\alpha = 0.41 \cdot A \cdot W_\alpha^{-1/3} \qquad (8)$$

Remember that Equation 7 (or Equation 8) is just the original fitted Equation 3 transformed to W_α under the most plausible of assumptions that W_α is $0.296 \cdot W_\infty$, the maximum of dW/dt, as represented by the VBGE, an equation that well describes the underlying two-part growth/reproduction process.

We call these Equations 7 and 8 the most basic of all because they predict M versus W_α across species, and adjust M to the relative size along the growth trajectory W/W_α within a species. Writing them this way focuses our attention on W_α, which is the most basic of life-history size variables, when an individual begins to allocate production to offspring and thus slows, if not stops, its growth. We will now show how life-history evolution sets W_α and how that relates to M_α.

The evolutionary optimal size at first reproduction (W_α) in a non-growing population

Four *main* problems dominate the study of life-history evolution (e.g. Stearns 1992): the size or age of first reproduction (W_α or α), the schedule for the allocation of personal production to reproduction after α, the size of an individual offspring (egg size in most fish) and ageing (senescence). If all personal production is devoted to reproduction at size W_α, growth ceases, and W_α is the adult size (called *determinate growth*). If only some of the personal production is devoted to reproduction at size W_α, growth (albeit slower) continues after age α (called *indeterminate growth*), generally leading to some W_∞ size. The relation between W_α and W_∞ depends upon the reproductive allocation schedule. Evolutionary models for optimal indeterminate growth are very complicated (e.g. Perrin and Sibly 1993; Charnov *et al.* 2001; Thygesen *et al.* 2005; Quince *et al.* 2008), and most trade-off assumptions do not favour indeterminate growth as the optimal life history. These numerous cases favour all production at W_α to be given to reproduction, resulting in W_α being the final adult size. The issue of determinate versus indeterminate growth is a complex one, and we will not develop it here.

What we will do is use life-history optimization to predict W_α in the face of a simple pre-reproductive growth function and size dependence for pre-reproductive mortality. Let us derive the optimal adult body size, W_α, for a very simple, determinate growth life history. Of course, fish are not this simple, but the model has several fundamental features in common with more complex, indeterminate growth cases, and this model is very simple to understand. Suppose juvenile growth follows the production law $\frac{\mathrm{d}W}{\mathrm{d}t} = A \cdot W^{0.67}$. Suppose an individual grows until some size W_α, when it then *gives all of* dW/dt *to offspring production* and thus stops growing; W_α is the adult size. dW_α/dt, the mass given to reproduction per year, is usually called *the reproductive allocation* (*RA*).

What determines the optimal W_α? It's mortality and growth, of course. The mortality rate of young immatures is generally very high; suppose that, after an initial burst of density-dependent death that stabilizes recruitment, the mortality rate declines with increasing immature body mass according to the rule $M = D_i \cdot W^{-h_i}$, where i refers to species i (this size rule may apply only after some small size is reached). We allow various species to have differing D and h variables, but all have some size dependence ($h = 0$ is okay, too). Notice that this mortality is imposed externally to the organism (its predators, competitors, etc.); we leave unspecified where it comes from. All that a growing organism can do is decide at what size (age) to quit growing and begin reproducing (W_α). On the one hand, the longer it delays initiating reproduction, the greater its cumulative chance of dying without reproducing at all (a cost). On the other hand, however, the longer it delays, the greater its reproductive ability, as it gives dW/dt to reproduction, its own growth capacity, which is $A \cdot W^{0.67}$ (a benefit). The optimal W_α balances this cost (risk of death) and benefit (reproduction rate).

Life-history theory (Stearns 1992) requires us to choose a measure of Darwinian fitness to carry out this optimization. Numerous possibilities exist (Stearns 1992; see also Metz *et al.* 2008), but the choice really mostly depends upon our population dynamics assumptions (e.g. Charnov 2009). Non-growing populations lead to the net reproductive rate (R_0) being the appropriate fitness measure, and growing populations lead to the intrinsic rate of increase, labelled '*r*,' being the fitness measure; populations in highly variable environments may require stochastic versions of R_0 or '*r*. Here we assume non-growing populations and use R_0 as fitness. R_0 here has some very general and unusual *multiplicative* properties, which we derive and discuss in Appendix 2. For the simple determinate growth life history modelled here, R_0 takes a very simple form:

$$R_0 = \frac{b \cdot e^{-\int_0^\alpha M(x)\mathrm{d}x}}{M_\alpha} \tag{9}$$

where the exponential is the chance of living to reproduce at age α (often called S(α)), the $1/M_\alpha$ is the average adult lifespan, and b is the egg production per unit of time while an adult.

$$b = \frac{A \cdot W_\alpha^{0.67}}{C_1}, \tag{10a}$$

because offspring production is just diverted self-growth and C_1 is the mass of each egg. Of course,

$$M_\alpha = D \cdot W_\alpha^{-h} \tag{10b}$$

(dropping the i subscript).

R_0 can now be written as:

$$R_0 = \frac{A \cdot W_\alpha^{0.67} \cdot e^{-\int_0^\alpha M(x)\mathrm{d}x}}{C_1 \cdot D \cdot W_\alpha^{-h}} \tag{11a}$$

or

$$\log_e R_0 = \log_e\left(\frac{A}{D \cdot C_1}\right) + (0.67+h) \cdot \log_e(W_\alpha) - \int_0^\alpha M(x)\mathrm{d}x. \tag{11b}$$

The optimal W_α is where $\partial \log_e R_0/\partial\alpha = 0$.

This is when

$$\partial log_e R_0/\partial\alpha = \frac{(0.67+h)\frac{\mathrm{d}W_\alpha}{d\alpha}}{W_\alpha} - M_\alpha = 0,$$
$$\text{as } \frac{d[\int_0^\alpha M(x)\mathrm{d}x]}{d\alpha} = M_\alpha$$

and $\log_e\left(\frac{A}{D \cdot C_1}\right)$ is just a constant.

As $\frac{\mathrm{d}W_\alpha}{d\alpha} = A \cdot W_\alpha^{2/3}$ we have $\frac{(0.67+h)A \cdot W_\alpha^{2/3}}{W_\alpha} - M_\alpha = 0$, which gives

$$M_\alpha = (0.67+h)A \cdot W_\alpha^{-1/3} \tag{12}$$

Equation 12 is equivalent in *form* to empirical Equation 8, excepting the constant multiplier of A, which is (0.67 + h) here and 0.41 fitted for the indeterminate growing fish; our model assumption of determinate growth causes this numeric difference in the normalization constant. Equation 12 may, of course, be solved for W_α.

Notice that the only mortality (M) appearing in the final answer (Equation 12) is M_α; all the earlier mortality, including density-dependent mortality very early in life, has gone away. This is a generic feature of R_0 maximization, which sets up this special relation between M_α and W_α (e.g. Charnov 1993). However, we can recover M values at some earlier ages/sizes through the $M = D \cdot W^{-h}$ function. If we pick some other W, say W_y, we have as follows:

$$M_y = D \cdot W_y^{-h} \text{ and}$$

$M_\alpha = D \cdot W_\alpha^{-h}$ giving

$$\frac{M_y}{M_\alpha} = \left(\frac{W_y}{W_\alpha}\right)^{-h} \text{ or } M_y = \left(\frac{W_y}{W_\alpha}\right)^{-h} \cdot M_\alpha$$

or, from Equation 12:

$$M_y = (0.67+h)\left(\frac{W_y}{W_\alpha}\right)^{-h} \cdot A \cdot W_\alpha^{-1/3} \tag{13}$$

Equation 13 is the same *form* as empirical Equation 7; we predict M_y at sizes other than W_α by multiplying the M_α equation by $\left(\frac{W_y}{W_\alpha}\right)^{-h}$, the relative mass ratio raised to the power $-h$, the exponent of M vs. W along the growth trajectory. For determinate growers, this applies to the smaller W. A similar principle for adjustment of M_y to W_y would apply for other $M_y = g(W_y)$ functional forms.

Suppose A is greatly affected by temperature (or, say, diet or foraging mode); then that A will simply match W_α to the prevailing M function. In a basic sense, temperature or diet effects on the optimal W_α are already accounted for in A (Charnov and

Gillooly 2004). The temperature term was not significant when added to Equation 1, most likely because temperature was already present when K was in the equation $\left(\text{recall, } K = \left(\frac{A}{3}\right) W_{\infty}^{-1/3}\right)$.

Mortality (M) need not have a particular size-based form during growth, and our optimal life-history scheme works just as well if the M is independent of size; simply set $h = 0$ in Equation 13. So, the theory does not predict h, and it simply takes it as an input from the environment. For each species, natural selection matches W_α to the environmentally given M_α (or M schedule) based on A, the height of the production function. Thus, M_α and W_α are brought into a very special relation with each other (Equation 12). Both A and 'h' may vary among species/habitats, and this will introduce between-species variation into the multiplier of $W_\alpha^{-1/3}$ in Equations. 12 and 13. We suspect that pooling species with various (h) in a single data fit will reduce the correlation and simply predict some sort of average h.

Expanding this fitness optimization model to full indeterminate growth is a formidable task, and we will not do it here. Charnov *et al.* (2001) and Charnov and Gillooly (2004) show that A enters the M_α, W_α power function in exactly the same way as in Equation 12 in a model that yields indeterminate growth as the optimum. What is expected to differ between determinate and indeterminate growth is the multiplier of $A \cdot W_\alpha^{-1/3}$, the 'non-A' part of the normalization constant.

Discussion: $M_\alpha/K \approx 1.8$ implies a general $M_\alpha \cdot \alpha$ rule for indeterminate growers

Charnov (1993, p. 61) noted the following identity for the VBGE, where age of first reproduction, α, is measured from size zero: $\frac{L_\alpha}{L_\infty} = 1 - e^{-K \cdot \alpha} = 1 - e^{-(K/M_\alpha)(\alpha \cdot M_\alpha)}$. Any life-history optimization model where the resulting lifetime growth is adequately described by the VBGE (thus setting $\frac{L_\alpha}{L_\infty} \approx 2/3$) *and* which sets $\alpha \cdot M_\alpha \approx 2$, the typically observed fish (and reptile) value (Charnov 1993, Chapter 4), makes the following prediction:

$$(\alpha \cdot M_\alpha) \cdot \left(\frac{K}{M_\alpha}\right) = 1.1$$

or

$$\frac{M_\alpha}{K} = \frac{2}{1.1} = 1.82$$

We may not understand just what trade-offs favour indeterminate growth in fish, but $\alpha \cdot M_\alpha \approx 2$ is the necessary result to predict the correct M_α/K number. This is worth remembering.

Discussion: across-species life histories, power functions are not (always) allometries

In this section, we further use the determinate growth approximation for fish. Let $\frac{dW}{dT} = A \cdot W^{0.67}$. At maturation size W_α, the organism will be giving $\frac{dW_\alpha}{dT} = A \cdot W_\alpha^{2/3}$ mass to reproduction per unit of time (its *reproductive allocation, RA*). *Reproductive effort* (*RE*) is usually defined as RA divided by body mass (e.g. Stearns 1992; Charnov *et al.* 2007), so $RE = \frac{dW_\alpha}{W_\alpha \cdot dT} = A \cdot W_\alpha^{-1/3}$. Integrating the determinate growth equation from $W = 0$ at $T = 0$ shows that $[3/A] \cdot W_\alpha^{-1/3} = \alpha$, where α is the age of first reproduction; Appendix 1 shows that solving the VBGE for the age at first reproduction when $W_\alpha/W_\infty = 0.296$ gives a similar result: $\alpha \propto \frac{W_\alpha^{1/3}}{A}$.

So, we have power functions for three key life-history variables (α, M_α, RE):

$$M_\alpha \propto A \cdot W_\alpha^{-1/3} \tag{14a}$$

$$RE = A \cdot W_\alpha^{-1/3} \tag{14b}$$

$$\alpha = \frac{3}{A} \cdot W_\alpha^{1/3} \tag{14c}$$

Equations 14a, b and c are three of the four central variables used to describe fish life histories: α is just the accumulated growth function, RE is just the turning of personal growth at W_α into production of offspring and M_α is because of the optimization of W_α in the face of mortality. To obtain yearly offspring production (call it b), just divide $RA = A \cdot W_\alpha^{2/3}$ by the mass of an egg, C_1:

$$b = \frac{A \cdot W_\alpha^{2/3}}{C_1} \tag{14d}$$

Each of the four power functions that sit at the centre of how we describe life histories generalizes to indeterminate growth life histories (with generally different multipliers of A). Every one of them contains A. Thus, they will form across-species ⅓, ⅔ allometries only if all the species in the data set have the same A. If the species differ a lot in A, across-species plots may not look much like (−⅓, ⅓, ⅔) power functions; the ⅔ scaling of yearly clutch size also requires that egg size be similar across species (or at least uncorrelated with W_α across species). In all cases, we expect good allometries (across-species ⅓, ⅔ power functions) if we correct

α, RE, M_α, or b by dividing (for α multiplying) by A. Of course, if A is *itself* a power function of W_α, across-species plots will be allometries that combine the two exponents. The plotting of M_α vs. K is equivalent to correcting M_α by A across species, which is why plots of M_α vs. K are so much tighter than plots of M_α vs. L_∞ (or W_∞) (e.g. Cury and Pauly 2000), where A varies among the data points.

Clearly, understanding A is a central question in the study of fish life histories; fortunately, we can estimate A as $3 \cdot K \cdot W_\infty^{1/3}$ (Equation 5c) whenever we describe fish growth with the VBGE. We should plot A versus foraging mode, food type and temperature; we should determine whether A varies consistently with other habitat features, body size itself or perhaps phylogeny. Various scaling rules are known for how K varies with $L_\infty\left(\text{or } W_\infty^{-1/3}\right)$ within pelagic and demersal fish (Gislason *et al.* 2008, 2010), and we will develop these in relation to A in a later study. Perhaps A and M are themselves interrelated; if higher A often requires more foraging movement, then perhaps M will be driven up too.

Pauly (1981), reviewed in Cury and Pauly 2000) suggests that O_2 is the resource limiting growth in water-breathing animals, and thus, gill surface area and function determines 'A'. While we think this unlikely as a universal limiting factor, perhaps the morphology of gills can be used to estimate A, as gill structure is likely to be adjusted to ensure delivery of the needed quantity of oxygen for production, independent of what actually limits production.

Discussion: egg size, C_1

Egg size (individual offspring size, C_1, in mass) was dropped out of the optimization of R_0 argument, leading to Equation 12. This is why we could ignore egg size in this evolutionary scheme; egg size and $\{\alpha$, M_α or reproductive effort (RE)$\}$ are effectively uncoupled. What determines C_1 is very complicated. The key trade-off is clearly that of egg size and egg number; larger eggs mean fewer of them (Smith and Fretwell 1974). We know how to solve for the optimum (Smith and Fretwell 1974), and we know that optimal C_1 is expected to be usually independent of the total resources being devoted to eggs. What we do not know is how the trade-off structure for individual performance vs. egg size maps to the environment in which the eggs and young juveniles develop, although Wootton (1994) has made a splendid attempt to predict optimal egg size for pelagic marine fishes using these principles. Having said that, we do know many things about egg sizes in nature; for example, they are small for pelagic fish, larger in freshwater, larger with male parental care, sometimes changes seasonally and so forth (excellent review in Freedman and Noakes 2002). Generally, across species, they do not correlate with adult size except when adult size itself correlates with the spawning/larval development environment (e.g. spawning season), and the same rules probably apply to egg size vs. body size within a species (Fleming and Gross 1990). We have every reason to believe that natural selection can easily change egg size to match a local optimum (e.g. Fleming and Gross 1990; for salmon). Downhower and Charnov (1998) found that the average egg size in *Gambusia hubbsi* in the Bahamas was a constant with adult size within populations, but the average egg size (volume, mass) varied by a multiplier of five between isolated populations – remarkable size variation that is yet unexplained. We are lucky that the decoupling of egg size from evolutionary optimization of W_α allows us to treat egg size as a constant that drops out when we set $\frac{d(log_e R_0)}{d\alpha} = 0$.

Discussion: how shall we classify life histories, lifestyles and habitats?

The mostly widely used scheme to classify habitats (and lifestyles) with respect to fish life histories is that of Winemiller and Rose (1992), a variant of r/k selection theory. All such classification schemes map the habitat to the expected life history through assumptions about how natural selection operates there to favour that particular life history. Our life-history assembly rules in Equation 14a–c suggest that to map the environment to the life history, we need to know A, the height of the individual's production function, and M, the externally imposed mortality risk. As M (or more precisely M_α) must be very hard to know, it is not too surprising that it is not generally included as a feature of the habitat; it should be.

Equations 14 suggest a classification scheme with M on one axis and A on the other, illustrated in Fig. 2a. Each ray from the origin corresponds to a fixed value of $W_\alpha^{1/3}$, as Equation 14a has $W_\alpha^{1/3} \propto \frac{A}{M_\alpha}$; this is the optimal W_α in the face of A & M_α. Notice that for fish of the same body shape, $W_\alpha^{1/3} \propto L_\alpha$, so body length at first reproduction is the same along each ray. And, of course, steeper

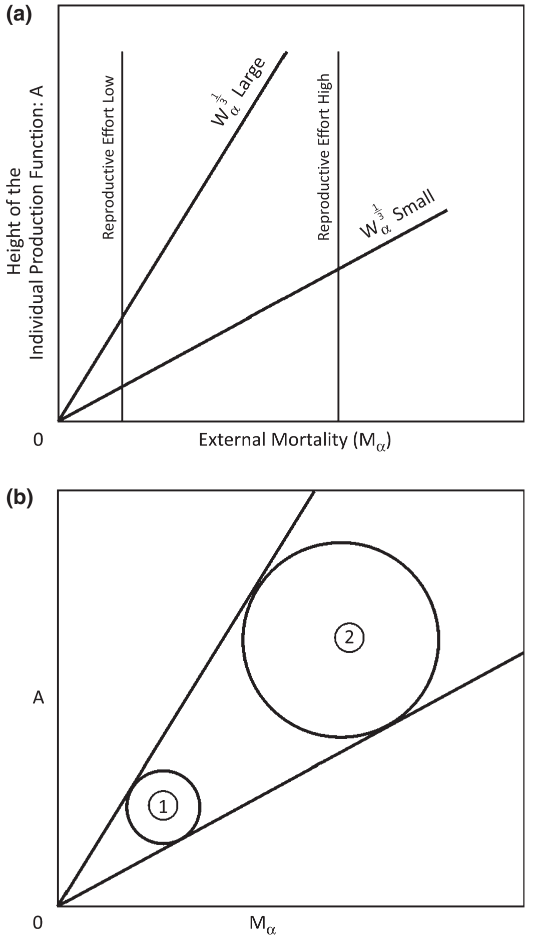

Figure 2. A scheme to classify life histories. (a) This square plots height of the growth curve (A) on the y axis and mortality near adulthood (M_α) on the x axis. Lines of equal body size $\left(W_\alpha^{1/3} = L_\alpha\right)$ are just rays from the origin. Reproductive effort is proportional to M_α, independent of A or W_α. (b) Hypothetical plot of two 'habitats' ① and ② on the A, M_α plane. Because both span the same A/M_α range, the two habitats will contain similar body sizes. *But* all the reproductive efforts will be high in ② and low in ①.

rays correspond to bigger $L_\alpha\left(W_\alpha^{1/3}\right)$. Equations 14a and 14b together imply that reproductive effort, RE, is $\propto M_\alpha$ independent of A or W_α. Thus, lines of equal *RE* are just vertical lines (parallel to the A axis); high M_α means high *RE*, and low M_α means low *RE*. Fig. 2a is a schematic of this classification scheme.

Different environments/habitats/foraging modes may impose different ranges for A and M. Fig. 2b shows how this scheme might work between habitats to predict life histories. In this hypothetical example, Habitat 1 has low A and low M, while Habitat 2 has high A and high M. Both habitats will have similar size ranges for $W_\alpha^{1/3} (= L_\alpha)$, but all the reproductive efforts will be low in Habitat 1 and high in Habitat 2. Clearly, the distribution of life histories we see depends upon how A and M are correlated with each other across habitats; Fig. 2b illustrates a positive A and M correlation.

The scheme of Equations 14a–c and Fig. 2 has one very unusual feature; suppose the average length of the adult life span is $\approx \frac{1}{M_\alpha}$, then (reproductive effort) (average adult life span) is RE/M_α and, by Equations 14a and b, is predicted to be approximately constant for all fish, independent of W_α or A. Lifetime reproductive effort (LRE) obeys the rule (approximately) among mammals and lizards (Charnov *et al.* 2007). Gunderson (1997) found the same relation in a diverse collection of 28 marine fish species, although his numeric LRE value is different from the mammals and reptiles.

Of course, Fig. 2 is incomplete to fully classify fish life histories; there is a third axis, extending into the plane to plot the size of an egg (or newborn). But without a better understanding of the egg and larval environment, that axis/dimension is the most difficult of all to predict using natural selection arguments.

Charnov *et al.* (2001) aggregated the yearly offspring production in the Winemiller and Rose (1992) data set to estimate the average yearly mass given to reproduction as a function of W_α across species (essentially reproductive allocation, *RA*). The data plot was uncontrolled for variation in A among the species, yet it showed a very strong ($r^2 = 0.74$, $n = 139$) power function form with a slope of ≈ 0.8. Thus, the species viewed as very different by Winemiller and Rose (1992) satisfy a *RA* vs. W_α scaling rule similar to that predicted by Equation 14; the species differ mainly in how the RA is divided among spawning batches, and of course, egg size. We agree with W–R that large-bodied species usually have long lifespans and much reproductive allocation when compared with small-bodied species and that offspring size relates to many identified features of the parental care/larval development environment. We believe that much of this between-species variation can be best understood in the context of Fig. 2: production rates (A) in the face of mortality rates (M) determine W_α, and then, the *RA* divided by individual offspring size sets the yearly offspring number. Species only grow to large body size if external mortality rates are low; hence, their lifespan is long. All the variables in this study can be treated as 'average annual' values, and thus, they smooth over the annual cycle of production and mortality. Perhaps it is not necessary to suggest that small-bodied species are selected for fast intrinsic rates of increase, and maybe the non-growing population assumption, mandating R_0 as a fitness measure, is adequate for *all body sizes*.

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Appendix 1: Some useful properties of the Bertalanffy growth equation

The Bertalanffy growth (BG) equation is the most widely used descriptor of body size growth for fish (and other indeterminate growers). It's usual integral form (two parameters) is where $L = L_\infty(1 - e^{-K\cdot X})$ length, L_∞ = asymptotic length, X is age and K is the growth coefficient. In weight (W), the equation is $W = W_\infty(1 - e^{-K\cdot X})^3$. In this appendix, we review and point out some of the properties of the BG equation, beginning with the differential equation form for weight (W). We begin with $\mathrm{d}W/\mathrm{d}t$, as production is a mass-based process, even if fishery scientists usually work in terms of length.

The differential equation form of the BG equation is as follows:

$$\frac{\mathrm{d}W}{\mathrm{d}t} = A\cdot W^{2/3} - B\cdot W \qquad (A1)$$

Length (L) is related to weight by the rule:

$$W = a\cdot L^3. \qquad (A2)$$

The asymptotic weight W_∞ is where $\frac{\mathrm{d}W}{\mathrm{d}t} = 0$, thus

$$W_\infty^{1/3} = \frac{A}{B}, \qquad (A3)$$

$$\left(\text{or } L_\infty = \left(\tfrac{W_\infty}{a}\right)^{1/3}\right).$$

Notice that Equation A2 allows us to write $\frac{\mathrm{d}W}{\mathrm{d}t} = a\cdot 3L^2\cdot\frac{\mathrm{d}L}{\mathrm{d}t}$ or $\frac{\mathrm{d}L}{\mathrm{d}t} = \frac{\mathrm{d}W}{\mathrm{d}t}\left(\frac{1}{a\cdot 3L^2}\right)$. Now, combining this with Equations A1, A2 and A3, we can show that $\frac{\mathrm{d}L}{\mathrm{d}t} = \frac{B}{3}[L_\infty - L] = K[L_\infty - L]$, so that $K = \frac{B}{3}$. This is the differential equation for length.

As $K = \frac{B}{3}$ and $W_\infty^{1/3} = \frac{A}{B}, K = \left(\frac{A}{3}\right)W_\infty^{-1/3}$ so that

$$\log K = \log_e\left(\frac{A}{3}\right) - 1/3\log_e W_\infty. \qquad (A4)$$

We can use Equation A2 to transform W∞ to L∞ :

$$\begin{aligned} K &= \left(\frac{A}{3}\right)\left(\frac{1}{a^{1/3}}\right)\cdot L_\infty^{-1} \\ \log_e K &= \left[\log_e\left(\frac{A}{3}\right) - \frac{1}{3}\log_e a\right] - \log_e L_\infty \end{aligned} \qquad (A5)$$

A, of course, is estimated as $A = 3\cdot K\cdot W_\infty^{1/3}$. We can estimate A from the K, L_∞ data if we know the shape coefficient of Equation A2.

What Is *A* in the BG Equation?

As A of $\mathrm{d}W/\mathrm{d}t$ is a key parameter, it seems worthwhile to ask what it means. In von Bertalanffy's original derivation, the $A\cdot W^{2/3}$ term was anabolism, the building of *new* tissue. It is probably reasonably interpreted as reflecting the intake of nutrition (food), which is assumed to scale with $W^{2/3}$. The BW term is catabolism, the breakdown of tissue (*but* $B\cdot W$ also must include reproductive allocation; Charnov 2008). While fisheries scientists no longer accept the simple physiological interpretation of von Bertalanffy, it may well be useful to treat the $A\cdot W^{2/3}$ term as the scaling of new tissue production.

There is another way to interpret the A coefficient. Rewrite Equation A1 as

$$\frac{\mathrm{d}W}{\mathrm{d}t} = A\cdot W^{2/3}\left[1 - \frac{B}{A}\cdot W^{1/3}\right];$$

but by Equation A3,

$$\frac{\mathrm{d}W}{\mathrm{d}t} = A\cdot W^{2/3}\left[1 - \left(\frac{W}{W_\infty}\right)^{1/3}\right]. \qquad (A6)$$

Thus, $\frac{\mathrm{d}W}{\mathrm{d}t}$ is proportional to $W^{2/3}$ at any fixed W/W_∞ value with A (and the W/W_∞ term) determining the 'height' of the ⅔ power function. For example, at very small body size, $W/W_\infty \approx 0$ and Equation A6 becomes $\mathrm{d}W/\mathrm{d}t \approx AW^{2/3}$; A is the height of the power function ($W^{2/3}$) growth curve at small W.

A interpreted this way is also true for the size at fastest growth. The max of $\frac{dW}{dt}$ is where $\frac{\partial(dW/dt)}{\partial W} = 0$, which implies from Equation A1 that $\frac{2}{3}W^{-1/3}\cdot A - B = 0$. We combine this with Equation A3 for W_∞ to show that $W/W_\infty = 0.296$ (which $= (2/3)^3$) at the max of $\frac{dW}{dt}$. Putting this into Equation A6 shows that $\frac{dW}{dt} = \frac{A}{3}\cdot W^{2/3}$ at the size of fastest growth; thus, $A/3$ is the height of *this* ⅔ power function for $\frac{dW}{dt}$ at fastest growth. Table A1 shows a simple way to estimate $\frac{dW}{dt}$ at fastest growth ($W = 0.296\cdot W_\infty$).

Table A1 Max $\frac{dW}{dt}$

As $\frac{dW}{dt} = A/3\cdot W^{2/3}$ (Equation A7), we have $\frac{dW}{dt} = A/3(0.296\cdot W_\infty)^{2/3}$ at fastest growth. But $K = A/3\cdot W_\infty^{-1/3}$ (Equation A4), so that $\max \frac{dW}{dt} = (0.293)^{2/3}\cdot K\cdot W_\infty = 0.44\cdot K\cdot W_\infty$; the maximum growth rate is estimated by 0.44 of the product of K times W_∞.

Appendix 2: Fitness (R_0) is a product (derivation from Charnov 1997)

The 'net reproductive rate,' R_0, is defined as $R_0 = \int_0^\infty l(x)\cdot b(x)dx$ (Equation B1), and calculates the average number of daughters produced over a female's lifespan. ($l(x)$ is the probability of being alive at age x; $b(x)$ is the daughters produced at age x that are alive at independence from mother; $b > 0$ only if $x > \alpha$, the age at first birth, measured from independence.) Now, write $b(x) = b(y)$ for $y = x - \alpha$ and denote $l(x)$ for $x > \alpha$ as $l(x) = S(\alpha)\cdot e^{-\varphi(x-\alpha)} = S(\alpha)\cdot e^{-\varphi(y)}$. (Notice that $\varphi(y)$ is zero at $y = 0$ and is increasing with y; $\partial(-\log l(x))/\partial y = \partial\varphi(y)/\partial y$, so $\partial\varphi/\partial y$ is the instantaneous mortality rate at age y.) $S(\alpha)$ is the chance of living from independence to α. R_0 can be written for this general life history as:

$$R_0 = S(\alpha)\cdot\int_0^\infty b(y)\cdot e^{-\varphi(y)}dy \qquad (B2)$$

Recall from the stable age distribution theory that the proportion of the breeding lifespan spent between ages y and $y + dy$ (the probability density function for the adult ages) is given by:

$$\frac{e^{-\varphi(y)}dy}{\int_0^\infty e^{-\varphi(y)}dy}$$

Now, multiply Equation (B2) by:

$$\frac{\int_0^\infty e^{-\phi(y)}dy}{\int_0^\infty e^{-\phi(y)}dy}$$

to yield:

$$R_0 = S(\alpha)\left[\int_0^\infty b(y)\cdot\frac{e^{-\varphi(y)}}{\int_0^\infty e^{-\varphi(y)dy}}dy\right]\left(\int_0^\infty e^{-\varphi(y)dy}\right) \qquad (B3)$$

$S(\alpha)$ is the chance of living to reproduce at age α, while the term in square brackets is simply $\bar{b}$, the average rate of production of offspring over the reproductive adult life, and the term in curved brackets is simply $E(\alpha)$, the expectation of further life at age α, the average length of the adult lifespan. So, Equation (B3) is really:

$$R_0 = S(\alpha)\cdot\bar{b}\cdot E(\alpha) \qquad (B4)$$

Equation (B4) applies to any *age-structured* life history; R_0 is the simple product of three aggregated terms, each an average. For Equation (B4) to be used as a fitness measure, the population must not be growing. This makes $R_0 \approx 1$ for typical individuals, owing to density dependence. But mutant individuals may have their own $R_0 \neq 1$, and it is fitness and trade-offs for mutants, which are discussed here. Thus, we use R_0, Equation (B4), as a fitness measure, with the condition that it must equal unity at the optimum, when mutants are the same as typical (wild type).

Evolutionary ecologists often prefer to work with a version of Equation A4 where $b(y) = \frac{R(y)}{m_0}$; $R(y)$ is the mass allocated to reproduction at age y, while m_0 is the size of each offspring. Then Equation B4 becomes

$$R_0 = \frac{S(\alpha)}{m_0}\cdot\bar{R}\cdot E(\alpha) \qquad (B5)$$

A further common step is to make $R(y)$ body-size dependent.

Notice that if the adult instantaneous mortality rate (M) is an age-independent constant (M_α), $E(\alpha)$ is simply $1/M_\alpha$; when combined $\bar{b} = b$, this yields $R_0 = \frac{b\cdot S(\alpha)}{M_\alpha}$, Equation 9 in the text. See Metz *et al.* (2008) for a discussion of fitness measures.