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Size and Temperature in the Evolution of Fish Life Histories¹

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SYNOPSIS. Body size and temperature are the two most important variables affecting nearly all biological rates and times, especially individual growth or production rates. By favoring an optimal maturation age and reproductive allocation, natural selection links individual growth to the mortality schedule. A recent model for evolution of life histories for species with indeterminate growth, which includes most fish, successfully predicts the numeric values of two key dimensionless numbers and the allometry of the average reproductive allocation versus maturation size across species. Here we use this new model to predict the relationships of age-at-maturity, adult mortality and reproductive effort to environmental temperature and maturation size across species. Age-at-maturity, adult mortality and the proportion of the body mass given to reproduction per year are predicted to show ± 0.25 power allometries with mass at maturity, and an exponential (Boltzmann) temperature dependence. Temperature is assumed to affect only body size growth, so the temperature linkages of maturation, mortality and reproductive effort are indirect via life history optimization; this is briefly contrasted with the idea that (for example) temperature directly affects mortality.

INTRODUCTION

Fitness optimization and game theory (ESS) models have long been used to understand the evolutionary adjustment of life-history parameters in fish. Examples include age-at-sex-change in sequential hermaphrodites (Warner *et al.*, 1975), frequencies of alternative reproductive strategies among males (Gross and Charnov, 1979), egg size (Wootton, 1994; Charnov and Downhower, 1995), age and size at maturity (Roff, 1984; Schaffer and Elson, 1975; Stearns, 1992; Jensen, 1996) and reproductive effort (Reznick, 1983, 1996; Gunderson, 1997). Life-history theorists (*e.g.*, Stearns, 1992) often talk about the “General Life History Problem” by which they usually mean the co-adjustment by natural selection (=fitness optimization) of the age (size)-of-first-breeding *and* the reproductive allocation thereafter. Indeterminate or continued growth after the initiation of reproduction is thought to result from not all resources being diverted to reproduction, and the resulting body-size growth curve is due to the individual’s productive capacity blended with the reproductive allocation decisions. This paper reviews a recent fitness optimization model for the general life-history problem in fish (Charnov *et al.*, 2001), and then extends the model to make predictions about the relations between body size, environmental temperature, mortality rates, reproductive effort, and age-at-maturity.

OPTIMAL LIFE HISTORY

Individual production (growth) prior to the initiation of reproduction is assumed to follow the differential equation proposed by West *et al.* (2001),

$$\frac{dm}{dt} = am^{.75} - bm, \quad (1)$$

where m is mass and b is the maintenance metabolic rate per existing cell divided by the cost of building a new cell. To add reproduction to this equation, Charnov *et al.* (2001) suggested that after the onset of reproduction (at age α , size m_α), the quantity $c \cdot m$ mass is given to reproduction per unit of time; so, prior to maturation, growth follows eq. 1, and after maturation, growth follows eq. 1 minus $c \cdot m$. This is illustrated in Figure 1, where growth follows the hatched area. Charnov *et al.* (2001) further developed the idea that b and c were linked together in a trade-off: higher c required higher b , so that $c/b = q$. For non-growing populations, a female’s fitness is given by the net reproductive rate (R_0), the average number of offspring produced over a female’s life span, or $R_0 = \int_{\alpha}^{\infty} L_t \cdot b_t \cdot dt$, where L_t is the chance of being alive at age t and f_t are the offspring produced at that age. For a fixed offspring (egg) size (I), $f_t = c \cdot m_t / I$ or $f_t \propto c \cdot m_t$; thus,

$$R_0 \propto \int_{\alpha}^{\infty} L_t \cdot c \cdot m_t \cdot dt. \quad (2)$$

We assume (Fig. 2 in Charnov *et al.*, 2001) that the instantaneous mortality rate is high (and density dependent) for small t , but drops to some constant value (Z) prior to feasible ages of maturation. Equation 2 is then written straightforwardly in terms of α , survival to age α , Z , q , b , a , and body size at age t (m_t). The equation is very complicated and so is the search for the optimal life history, which is assumed to set $\partial R_0 / \partial \alpha = 0$ and $\partial R_0 / \partial c = 0$. Thus, the optimal life history optimizes fitness with respect to age at first reproduction, α , and reproductive allocation, c (see Charnov *et al.*, 2001 for the details).

The optimal life history takes a very simple form, shown in Figure 2. The value of q determines the optimal values of the two dimensionless numbers, $\alpha \cdot Z$ ($=C_1$) and b/Z ($=C_3$), thus setting the number $b \cdot q / Z = c / Z$ ($=C_2$). These optimal dimensionless numbers are independent of the value of a , the coefficient of the

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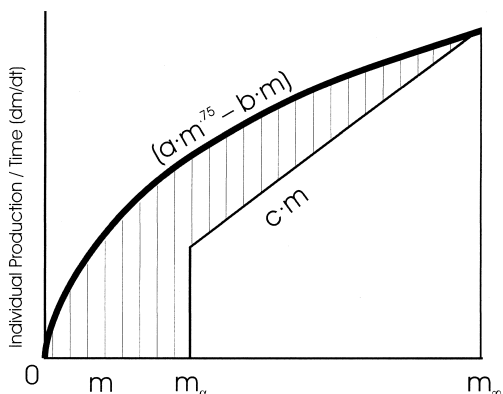


FIG. 1. Schematic diagram of the growth model (dm/dt , m = mass). Growth prior to maturation (m_α) follows the West *et al.* (2001) production relation (thick line). After maturation, $c \cdot m$ of production is given to reproduction, so growth then follows the thick line minus $c \cdot m$. Overall growth follows the hatched area. Natural selection is assumed to adjust α (or m_α) and c to maximize R_0 (from Charnov *et al.*, 2001) (text eq. 2).

first term in the production equation (eq. 1, Fig. 1). $\alpha \cdot Z$ has been estimated to be an invariant value of ≈ 2 for several fish data sets (discussed in Charnov, 1993), and Gunderson (1997) has estimated that c is indeed proportional to Z (there called M), so that $c/Z \approx 0.6$. Remarkably, Figure 2 shows that $\alpha \cdot Z$ near 2 predicts c/Z to be about 0.6, the observed value.

Charnov *et al.* (2001) also show that if \bar{P} is the average mass given to reproduction per unit of time by the adults, the optimal life history can be expressed as:

$$\bar{P} = a m_\alpha^{0.75} \phi(\cdot)$$

where $\phi(\cdot)$ is a dimensionless function of q , $\alpha \cdot Z$ and b/Z . Since these dimensionless numbers are predicted (Fig. 2) to be constants across species, we have $\bar{P} \propto a \cdot m_\alpha^{0.75}$, a 0.75 scaling of average reproduction allocation (\bar{P}) on maturation size (m_α) for a collection of species with the same (similar) a values. A large data set (139 temperate zone species) showed just such a log linear relation with a high correlation ($r = 0.86$) and a slope (exponent) not different from the predicted 0.75 (Charnov *et al.*, 2001).

OPTIMAL RELATIONSHIP BETWEEN α , c , Z , AND m_α

Equation 1 may be integrated from time zero (size $m_0 \sim 0$) to time α (size m_α) to give (West *et al.*, 2001):

$$m_\alpha^{0.25} = \left(\frac{a}{b}\right) [1 - e^{-\alpha(b/4)}]. \quad (3)$$

Since $(a/b)^4$ is the asymptotic size implied by Eqn. 1 (m where eq. 1 = 0), we may define the quantity μ as

$$\mu = \frac{m_\alpha^{0.25}}{\left(\frac{a}{b}\right)} = [1 - e^{-\alpha(b/4)}]. \quad (4)$$

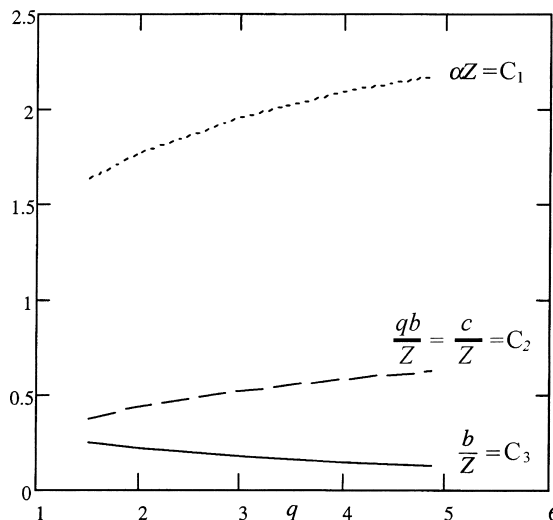


FIG. 2. The optimal life history sets the value of two dimensionless numbers, $\alpha \cdot Z$ and b/Z , as a function of q , the assumed trade-off between c and b ($c = q \cdot b$); thus, the optimal life history makes $c \propto Z$ (from Charnov *et al.*, 2001).

μ is expected to be an invariant since $\alpha \cdot b$ is an invariant ($= C_1 \cdot C_3$), as shown in Figure 2.

Notice that eqs. 3 and 4 combined with the invariance rules of Figure 2 (for $\alpha \cdot Z = C_1$, $b/Z = C_3$ and $c/Z = C_2$) imply:

$$\alpha = \left[\frac{-\ln(1 - \mu)}{\mu} \right] \left(\frac{4}{a} \right) m_\alpha^{0.25} \quad (5a)$$

$$Z = \left[\frac{C_1 \mu}{-\ln(1 - \mu)} \right] \left(\frac{a}{4} \right) m_\alpha^{-0.25} \quad (5b)$$

$$c = \left[\frac{C_1 C_2 \mu}{-\ln(1 - \mu)} \right] \left(\frac{a}{4} \right) m_\alpha^{-0.25}. \quad (5c)$$

So, α , reproductive effort (c), and adult mortality (Z) are all predicted to scale as ± 0.25 with mass at maturity (m_α) for species with the same a value. Since C_1 , C_2 and C_3 are predicted numerically (Fig. 2) at the optimal life history (e.g., $\alpha \cdot Z = C_1 \approx 2$ implies $C_2 \approx 0.6$ and $C_3 \approx 0.15$), the *intercepts* of the scaling lines are predicted if a is known.

BUT a DEPENDS ON ENVIRONMENTAL TEMPERATURE

Gillooly *et al.* (2001, 2002) gave theoretical argument and showed much data on metabolic rates and developmental times supporting the idea that $a = A \cdot e^{-E/k \cdot T}$, where T is degrees Kelvin, k is Boltzmann's constant, and E is the average activation energy for the rate-limiting biochemical reactions of metabolism fueling growth ($E \approx 0.6$ eV). Here A is a proportionality factor expected to be approximately constant within a taxa like bony fish. Some variation in A as been shown in zooplankton (Gillooly *et al.*, 2002) to covary with resource availability (*i.e.*, stoichiometry) of limiting nutrients (*e.g.*, phosphorus).

Notice that if we substitute $A \cdot e^{-E/k \cdot T}$ for a in Equation

5, in addition to the quarter-power mass dependence, we predict an exponential temperature dependence for α , c and Z , *even though temperature only directly affects a in this theory*. This leads to:

$$Z = \phi_1(C_1, C_3, A)e^{-E/kT}m_\alpha^{-0.25} \quad (6a)$$

$$\alpha = \phi_2(C_1, C_3, A)e^{E/kT}m_\alpha^{0.25} \quad (6b)$$

$$c = \phi_3(C_1, C_2, C_3, A)e^{-E/kT}m_\alpha^{-0.25}. \quad (6c)$$

Since the dimensionless numbers (Fig. 2) C_1 , C_2 and C_3 are independent of a , they are thus predicted to be *independent of temperature*. ϕ_1 , ϕ_2 and ϕ_3 are the intercepts of the temperature/body size relations for Z , α and c : since C_1 , C_2 and C_3 are predictable from life-history theory, fitting (discussed below) one of the three relations suffices to predict A , and thus predicts the intercepts for the remaining two relations.

For example, consider eq. 6a for Z . We can rewrite it in one of two ways:

$$\ln(Zm_\alpha^{0.25}) = \ln(\phi_1) - \frac{E}{kT} \quad \text{and} \quad (7a)$$

$$\ln(Ze^{E/kT}) = \ln(\phi_1) - 0.25 \ln m_\alpha. \quad (7b)$$

In words, eq. 7a means that the natural log of the size-corrected mortality rate should be linearly related to the temperature function $1/kT$ with a slope equal to minus the activation energy ($-E$), which should be about -0.6 (Gillooly *et al.*, 2001, 2002; Savage *et al.*, 2004). Eq. 7b means the natural log of the temperature-corrected mortality rate should show a -0.25 allometry with size at maturity (m_α). Eqs. 6b and 6c may be treated similarly. In the following section, we provide a *preliminary* test of eqn. 7a for the temperature and body-size dependence of Z .

PAULY'S DATA COMPILATION

Pauly (1980) compiled data on Z (there called M), mean annual environmental temperature ($^{\circ}\text{C}$, easily converted to degree Kelvin) and adult maximum size (mass = m_{\max}) for 175 populations (stocks) of 84 species of fish. No data are provided on maturation size, so here we assume that $m_\alpha \propto m_{\max}$, known to be approximately true for fish (Beverton and Holt, 1959; Charnov, 1993). Figure 3A shows that the log of the size-corrected mortality (eq. 7a) is indeed linearly related to the temperature function with an estimated slope of -0.45 , not too different from the expected -0.6 . Figure 3B shows eq. 7b; the log of temperature-corrected ($E = 0.45$ is used here) mortality scales as -0.23 with the log of body mass. While the correlations are not particularly strong, the slopes are close to those that are theoretically predicted.

DISCUSSION

Many biological rates (units of 1/time) such as Z show a temperature/body-size dependence proportional to $e^{-E/kT}m^{-0.25}$, while biological times such as α show a dependence proportional to $e^{E/kT}m^{0.25}$ (e.g., Gillooly *et al.*, 2001, 2002; Savage *et al.*, 2004). The

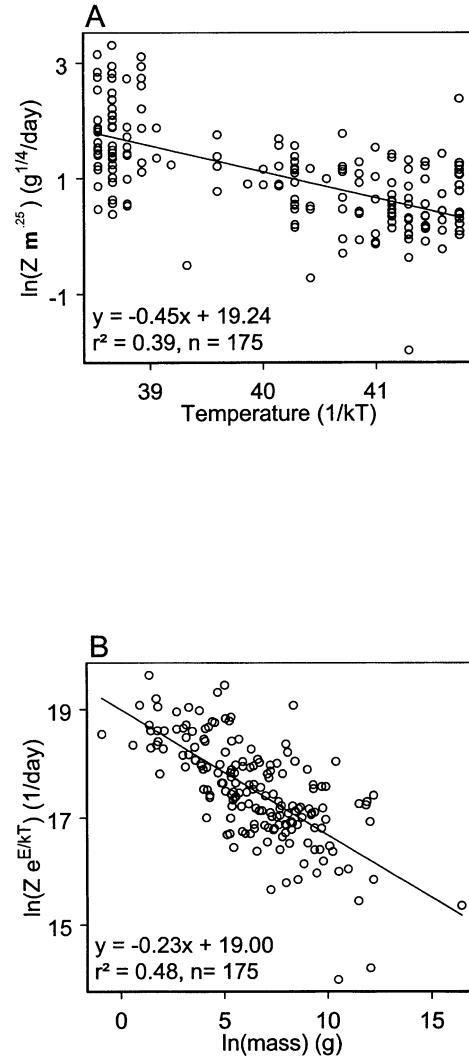


FIG. 3. (A) The relationship between mass-corrected instantaneous mortality rate and the yearly average environmental temperature function ($1/kT$; k = Boltzmann's constant; T = degrees Kelvin). From text eq. 7, we expect a negative, linear relation with a slope near 0.6 . (B) The relationship between the temperature-corrected instantaneous mortality rate ($E = 0.45$, as estimated in Fig. 3A) and body mass, estimated as asymptotic mass (m_{\max}). We expect, by text eq. 7, a linear relation with a slope of -0.25 (if $m_\alpha \propto m_{\max}$). Lines fit with type 1 linear regression. Data from Pauly, 1980.

present life-history model predicts *the* temperature and size dependence of Z , c , b , \bar{P}/m_α and α entirely through a mechanism of life-history optimization. The 0.25-power size dependence follows from the optimization shown in eq. 2, and holds for a collection of species with the same a value. The exponential temperature dependence described by the Boltzmann factor follows only from the effects of temperature on a , the height of the growth curve in eq. 1. Consider the mortality rate Z . The life-history theory allows Z to vary or not vary *directly* with temperature and still satisfy the temperature- and body-size dependence discussed above. This is because life-history optimization would adjust m_α to the a at any temperature matched to any value

of Z . Thus, Z determines m_{α} via natural selection in the face of the growth/production function (eq. 1; Charnov, 1993).

Note, however, some have argued that natural mortality rates are intrinsically determined through properties of organisms controlled by metabolic rate (*i.e.*, free-radical-caused cellular damage). Laboratory data showing that maximum life span in the absence of predation follows a Boltzmann-like temperature dependence appears to support these intrinsic causal factors (Gillooly *et al.*, 2001). Yet, the theory presented here *may* also predict this temperature dependence of maximum life span. This follows provided the investment in cellular maintenance that sets maximum life span is closely related to average adult life span (Z^{-1}) in the field. There is, in fact, evidence that supports this relationship. Beverton and Holt (1959) showed that Z^{-1} was correlated strongly with field maximum life spans in fish, while Charnov (1993, 2004) showed the same for mammals. Further research, including better data to estimate the intercepts of the scaling rules of eq. 6, is needed to address more fully whether mortality is somehow internally determined, or can be primarily considered external, as is done in the life-history theory developed here.

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