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Evolution of life history parameters in animals with indeterminate growth, particularly fish

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Summary

Most evolutionary life history theory is developed in terms of the allocation of resources to the competing ends of growth, reproduction, and survivorship. In this paper we show that certain dimensionless numbers may be used to describe the relationship between growth, maturation, and adult mortality; our theory aims to predict these numbers and we are led to aggregate some basic features of life histories, rather than explicitly considering the allocation of a limited resource to different components of fitness. The phenomenology developed here has the convenient property that only parameters describing the shapes of two assumed trade-offs among life history traits appear in the solution of the resulting optimisation problem. Comparative inter- and intraspecific data on fish, lizard, snake and shrimp populations suggest that this approach may help explain some common patterns in the life histories of animals with indeterminate growth.

Keywords: Dimensional analysis, body size allometry, ESS, evolution of maturation, growth curve evolution

Discussion

Thirty years ago Beverton and Holt (1959) and Beverton (1963) pioneered the comparative study of fish life histories by showing that within limited taxonomic boundaries (such as within the cod, salmon or herring family), there existed certain across-species (or populations within a species) patterns in growth and mortality. These patterns, reviewed in Cushing (1968) and Pauly (1980), are three in number. Within each group the adult instantaneous mortality rate, M, and the Bertalanffy growth coefficient, K, are positively related to each other so that the ratio K/M tends to be relatively constant; and the K/M ratio differs between taxa. The second pattern is that the length at maturity (l_α) is positively related to the Beralanffy asymptotic length (l_∞) so that the relative length at maturity, l_α/l_∞, tends to be a constant value within a taxa. K/M and l_α/l_∞ are themselves connected in an interesting way. If growth follows the two parameter Bertlanffy equation then

$$\frac{l_\alpha}{l_\infty} = 1 - e^{-K\alpha}$$

where α is the age of maturity. If a group of species share a common l_α/l_∞ value, they also share the same $K \cdot \alpha$ value; but if they also have K/M = constant, then the product $M \cdot \alpha$ will itself be a constant. Thus, species with the same K/M and l_α/l_∞ ratios will have adult instantaneous mortality rates (M) that are inversely proportional to the ages of maturity (α). Combining Beverton's (1963) Tables 4 and 10 shows that $M \simeq 2.1/\alpha$ for Clupeids and Engraulids (see also Roff 1984, Equation 37). The third pattern is that K and l_∞ are negatively related across species (or populations) within a closely related group. Pauly (1980; Munro and Pauly 1983; Pauly and

Munro 1984; Moreau *et al.* 1986; reviewed in Chapter 9 of Longhurst and Pauly 1987) showed that plots of $\log_e l_\infty$ versus $\log_e K$, among closely related species or populations within a species, are generally linear with slopes clustering near $-1/2$ (see also Table 1). For example, such a plot for 100 populations of closely related Tilapia species gives a linear relation with a functional regression (Ricker 1973) slope of -0.57 (Moreau *et al.*, 1986). Table 1 shows regression analysis for 11 other species.

Table 1. Estimates of h from within species regressions of $\log_e l_\infty$ on $\log_e K$.

Family/species	h^1	Standard error of h	Correlation coefficient/ sample size[2]	Probability level (2 tailed test)
Gadidae (Cod)				
1. *Gadus morhua*	0.55	0.06	$r = -0.65, n = 49$	< 0.0001
2. *Melanogrammus aeglefinus*	0.75	0.14	$r = -0.78, n = 13$	< 0.002
3. *Merlangius merlangus*	0.40	0.021	$r = -0.87, n = 91$	< 0.0001
Clupeidae (Herring, Sardines)				
4. *Clupea harengus*	0.50	0.08	$r = -0.39, n = 39$	< 0.014
5. *Sardina pilchardus*	0.42	0.08	$r = -0.66, n = 18$	< 0.003
6. *Sardinops caerula*	0.41	0.08	$r = -0.54, n = 19$	< 0.02
7. *Sardinella aurita*	0.38	0.08	$r = -0.73, n = 13$	<0.005
8. *Brevoortia tyrannus*	0.49	0.06	$r = -0.67, n = 43$	<0.0001
Engraulidae (Anchovies)				
9. *Engraulis japonicus*	0.44	0.065	$r = -0.85, n = 15$	< 0.0001
10. *Engraulis encrasicholus*	0.31	0.06	$r = -0.66, n = 17$	< 0.004
11. *Engraulis mordax*	0.27	0.025	$r = -0.90, n = 26$	< 0.0001

[1] h is minus the slope of the functional regression (Ricker (1973) also called the major axis) of $\log_e l_\infty$ vs $\log_e K$ within a species, between populations and/or year classes (see Note 2). The within-species data were used to estimate the h^s because plots at higher taxonomix levels (e.g. within a family, or pooling all species) lead to higher values of h. We suspect that this effect results from larger species having higher A values (but it could also be a statistical artifact (Pagel and Harvey, 1988)).

[2] A datum is a separate population, stock or year class.

Beverton (1963) went beyond the basic description of the patterns and proposed that they must reflect the action of natural selection. In his words: ". . . An adaptive interpretation of the adjustment of growth and longevity might be explicable in simple Darwinian terms by supposing that it is an 'advantage' to the individual to complete as much as possible of its potential growth within its likely maximum life-span, this advantage being that which best enables its reproductive potential to be realised and so maximises the contribution of its progeny to future generations. But in this case the age at first maturity must also be adjusted to life-span; that this happens is shown in Figure 7 by the constancy of the ratio of length at first maturity to asymptotic length (l_α/l_∞)." We view the present paper as a development of Beverton's argument, recast in terms of evolutionary life history theory.

Our reasons for being interested in these patterns are first, that the within-taxa constancy of the dimensionless numbers K/M, l_α/l_∞ and $\alpha \cdot M$ has also been shown for three other groups of animals: snakes; lizards; and Pandalid shrimp (Charnov 1979, 1989; Charnov and Shine 1990) (and K/M is near 1 for many sea urchin species, Ebert, 1975) and, second, that an approach to life histories which classifies them using a few aggregated numbers would itself seem to be a useful exercise. Thus, our goal is to develop life history theory to predict the values of these

dimensionless numbers. See Charnov and Berrigan (1990) for how various life styles affect the $\alpha \cdot M$ number and Charnov (1991) for discussion of the utility of looking for life history generalisations in terms of dimensionless numbers. While we do not claim that the present modelling exercise is unique, the phenomenology developed leads in a rather simple and elegant way to the predicted constancy of the three dimensionless numbers, and attaches specific meaning to their particular numerical values.

Models in evolutionary genetics show that the average number of offspring produced over an individual's total lifespan (R_o) is a measure of Darwinian fitness in a non-growing population (Lande, 1982; Charnov, 1986; 1990). Consider a newborn female and define l_x as the probability she is alive at age x, and b_x as her birth rate, in daughters, at age x. Her lifetime production of daughters is $R_o = \int_\alpha^\infty l_x b_x dx$. We can rewrite R_o as $R_o = l_\alpha \left[\frac{\int_\alpha^\infty l_x b_x dx}{l_\alpha}\right]$; the term in brackets is the average number of daughters born over a female's adult lifespan, the 'Fisherian reproductive value' (Fisher 1930) of an age α (a just mature) female, and will therefore be labelled $V(\alpha)$. We thus have

$$R_o = l_\alpha \cdot V(\alpha) \tag{1}$$

To allow for the possibility that mortality decreases over the immature period, a common feature of life tables, write l_α as $l_\alpha = e^{-\int_0^\alpha M(x)dx}$, where $M(x)$ may decrease with x. Charnov (1989, 1990), building on a suggestion by Roff (1984, 1986), proposed that $V(\alpha)$ could often be represented as $V(\alpha) \propto l_\alpha^\delta$ (length at age α to the power δ). We also assume Bertalanffy growth
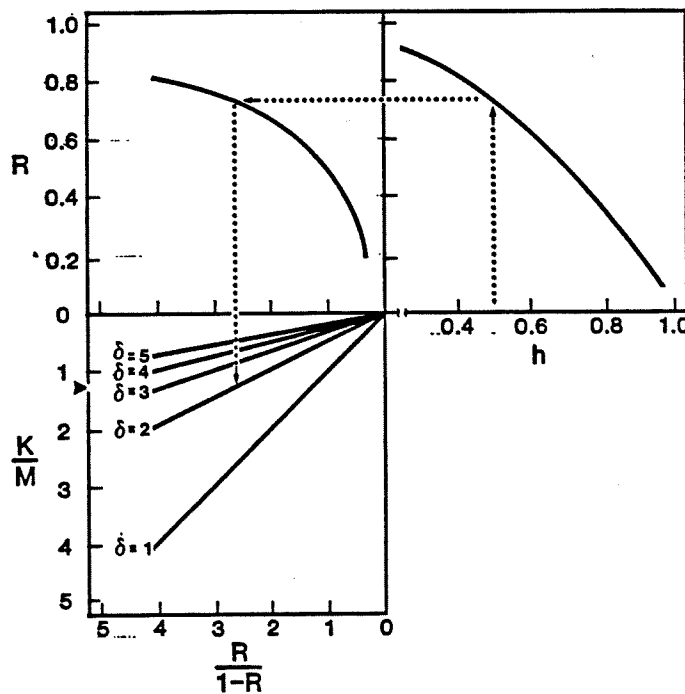

Figure 1. A graphical method to estimate the equilibrium $\frac{K}{M}$ and $\frac{l_\alpha}{l_\infty}$ $(= R)$ from δ and h (or vice versa); from Equation 3 and 4 in the text. The right hand panel is the solution of equation 3: R as a function of h. The upper left panel transforms R into $R/(1-R)$. The lower left panel is the solution to equation 4; it transforms $R/(1-R)$ into K/M for the appropriate δ value. The dotted lines show one example. Of course, the graphs also allow us to estimate δ and h from R and K/M.

$(l_x = l_\infty(1 - e^{-Kx}))$, and that l_∞ and K are inversely related as $l_\infty = A \cdot K^{-h}$ (with $h < 1$).

Putting the above into equation 1 gives

$$R_o \propto e^{-\int_o^\alpha M(x)dx} \cdot A^\delta \cdot K^{-h\delta}(1 - e^{-K \cdot \alpha})^\delta \qquad (2)$$

Natural selection acts on *this model life history through choice of* α *and* K. Evolutionary equilibrium is where $\frac{\partial \log_e R_o}{\partial \alpha} = 0$ and $\frac{\partial \log_e R_o}{\partial K}$ 0 at the same time. These operations on Equation 2 produce the following results; in what follows, M refers to $M(\alpha)$, the adult instantaneous mortality rate, assumed a constant over the adult lifespan (i.e. it stops decreasing at age α) and R refers to the relative length at the age of maturity $(R = \frac{l_\alpha}{l_\infty} = 1 - e^{-K \cdot \alpha})$:

$$[\frac{\partial \log_e R_o}{\partial K} = 0] \qquad h = \frac{R - l}{R} \log_e (1 - R) \qquad (3)$$

$$[\frac{\partial \log_e R_o}{\partial \alpha} = 0] \qquad \delta \cdot \frac{K}{M} = \frac{R}{1 - R} \qquad (4)$$

These two equations, as functions of the two shape coefficients δ and h, thus fix the value of two *dimensionless numbers*, K/M and l_α/l_∞ (= R). Three implications of these equations are noteworthy (see also Fig. 1).

First, Equation 3 has the following meaning: h must be < 1, and for a given h there is only one R ratio which satisfies the equation. Second, Equation 4 shows that for a given R and δ values, there is only one K/M ratio allowed; thus all species with the same h, δ values are predicted to have the same K/M ratio. Third, if we rewrite $-\log_e (1 - R)$ as $K \cdot \alpha$ and substitute it into Equation 3, we can combine this with equation 4 to show that $M \cdot \alpha = \delta \cdot h$ (Equation 5); the adult instantaneous mortality rate (M) is inversely proportional to the age of maturity, α, with the proportionality constant equal to $\delta \cdot h$.

If log regressions (functional regressions, Ricker 1973) of l_∞ on K can be used to estimate h, then the Pauly analysis mentioned earlier has h about the right magnitude ($\simeq 0.5$) since most fish have R in the range 0.4 to 0.8 (Beverton and Holt 1959), leading through Equation 3 to h being predicted to be in the range 0.4 to 0.8 (Fig. 1). This regression technique should give a valid estimate of h if: (i) the data come from populations with similar R values; and (ii) the height parameters in the particular trade-offs (the A of $l_\infty = A \cdot K^{-h}$) are the same and/or at least uncorrelated with either of two variables (l_∞ or K). Of course, functional regression (also called the major axis) assumes equal error variance on each axis; if more precise information is known about the respective error variances, other estimation schemes become more reasonable (Ricker, 1973; Pagel and Harvey, 1988). Our use of functional regression is motivated by the fact that between species (or population) variation in A (or $\log_e A$) contributes to error almost symmetrically on both axes. It should also be noted that the growth data used to estimate l_∞ and K (within each population) must span the entire age range; otherwise l_∞ and K will have a negative covariance due simply to the estimation of each from the same data.

Since h is predicted to be inversely related to R (Equation 3, Fig. 1), a powerful test of hypothesis would be to estimate the slope of the functional regression of $\log_e l_\infty$ on $\log_e K$ *within* groups of species (or populations) with similar R values, and then see if the relation between R and h looks like Equation 3. One comparison of this type is possible using the growth data compilation of Pauly (1978). He compiled or estimated growth curves for 1501 populations, stocks or year classes of 515 species of fish (in 104 families). Beverton and Holt (1959) and Beverton (1963) showed that R averaged $\simeq 0.55$ for the cod family (Gadidae) and $\simeq 0.75$ for the herring, sardines and anchovies (the Clupeomorpha, families Clupeidae and Engraulidae); these values for R are near the outer bounds for fish. From Equation 3 we predict $h \simeq 0.45$ for fish in the Clupeomorpha and $h \simeq 0.65$ for cod. From the Pauly (1978) compilation 11 species (three cods, five Clupeids, three Engraulids) have 13 or more observations per species (stocks and/or

year classes); Table 1 shows the results of functional regressions (Ricker 1973) of $\log_e l_\infty$ versus $\log_e K$ within each of these species. The estimates of h ranged from 0.27 to 0.75; Fig. 2 is a plot of the h, broken down by cod versus Clupeomorpha. Notice that the cod are generally much higher than the Clupeomorpha (the highest two h are cod) and the averages ($\bar{h}$), are not far from the theoretical expected: cod; theory = 0.65, observed = 0.57; Clupeomorpha; theory = 0.45, observed = 0.40. While this comparison involves few species (and while the within-family/ between-species differences are not explained), the averages do indeed provide support for the theoretical approach suggested here.
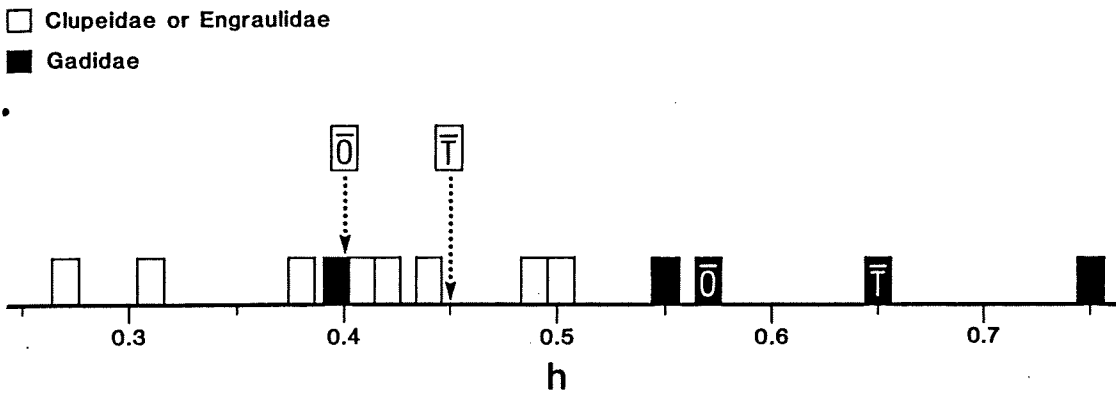

☐ **Clupeidae or Engraulidae**

■ **Gadidae**

Figure 2. A graphical representation of the h values of Table 1. In general, the cod (■) are higher than the Clupeomorpha (☐); the averages ($\bar{O}$ = observed; $\bar{T}$ = theoretical) are also shown.

The phenomenology developed here (Equation 2) aggregates the life history in two ways, first by assuming that $V(\alpha) \propto l_\alpha^\delta$, and second by assuming a growth trade-off of the form $l_\infty = A \cdot K^{-h}$. It leads to predictions as to the values of the desired dimensionless numbers (themselves aggregate variables), as functions of the shape coefficients δ and h. We consider this aggregate approach to life histories complementary to the more detailed, mechanistic approach adopted in most resource allocation models; it goes without saying that one might wish to derive the shape coefficients δ and h from more basic allocation principles (or even ignore the 'δ, h phenomenology' and use allocation principles directly to account for the data patterns of the dimensionless numbers – D. Roff (personal communication)). However, such aggregation, both in the theory (δ, h) and in the data (K/M, $\alpha \cdot M$, l_α/l_∞) may often allow us to see broader patterns (e.g. Charnov and Berrigan, 1990 for $\alpha \cdot M$). We end this note with one such puzzle about the K/M number; the between-species average K/M value for the Beverton–Holt (1959) fish data is near 1 or $K \simeq M$; this numerical relation, $K \simeq M$, is also true *on average* for snakes, for lizards, and even for sea urchins (Charnov and Shine, 1990; Ebert, 1975). Why should it be the case that $K \simeq M$ for such seemingly different animals? It is not true for Pandalid shrimp, where $K \simeq 0.37\,M$ (Charnov, 1989). And of course not all fish have $K \simeq M$; the clupeids have $K \simeq 0.67\,M$ (Beverton, 1963).

Acknowledgments

References

Beverton, R. J. H. (1963) Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. *Rapp. Proces-Verb. Cons. Intern. Explor. Mer.* **154**: 44–67.

Beverton, R. J. H. and Holt, S. J. (1959) A review of the lifespans and mortality rates of fish in nature and the relation to growth and other physiological characteristics. In *Ciba Foundation, Colloquia in ageing. V. The lifespan of animals.* pp. 142–77. Churchill, London.

Charnov, E. L. (1991) Non-dimensional numbers in the evolution of life histories. *Phil. Trans. Roy. Soc.* (Ser. B). In Press.

Charnov, E. L. (1990) On evolution of age of maturity and the adult lifespan. *J. Evol. Biol.* **3**: 139–44.

Charnov, E. L. (1989) Natural selection on age of maturity in shrimp. *Evol. Ecol.* **3**: 236–9.

Charnov, E. L. (1986) Life history evolution in a 'recruitment population': why are adult mortality rates constant? *Oikos* **47**: 129–34.

Charnov, E. L. (1979) Natural selection and sex change in Pandalid shrimp: test of a life history theory. *Amer. Natur.* **113**: 715–34.

Charnov, E. L. and Berrigan, D. (1990) Dimensionless numbers and life history evolution: age of maturity versus the adult lifespan. *Evol. Ecol.* **4**: 273–5.

Charnov, E. L. and Shine, R. (1990) Patterns of survivorship, growth and maturation in snakes and lizards. (Submitted, Amer. Natur.).

Cushing, D. H. (1968) *Fisheries biology*. Univ. Wisconsin Press, Madison, Wisconsin.

Ebert, T. (1975) Growth and mortality in post-larval echinoids. *Amer. Zool.* **15**: 755–75.

Fisher, R. A. (1930) *The genetical theory of natural selection*. Oxford Univ. Press, Oxford.

Lande, R. (1982) A quantitative genetic theory of life history evolution. *Ecology* **63**: 607–15.

Longhurst, A. R. and Pauly, D. (1987) *Ecology of tropical oceans*. Academic Press, N.Y.

Moreau, J., Bambino, C. and Pauly, D. (1986) Indices of overall growth performance of 100 Tilapia (Cichlidae) populations. In *The First Asian Fisheries Forum* (J. L. Maclean, L. B. Dizon and L. V. Hosillos, eds) pp. 201–6. Asian Fisheries Society, Manila, Philippines.

Munro, J. L. and Pauly, D. (1983) A simple method for comparing the growth of fishes and invertebrates. *Fishbyte* **1**: 5–6.

Pagel, M. D. and Harvey, P. H. (1988) The taxon-level problem in the evolution of mammalian brain size: facts and artifacts. *Amer. Natur.* **132**: 344–59.

Pauly, D. (1978) A preliminary compilation of fish length growth parameters. *Ber. Inst. f. Meeresk. Univ. Kiel.* **No.55**, 1–200.

Pauly, D. (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. Cons. Int. Explor. Mer.* **39**: 175–92.

Pauly, D. and Munro, J. L. (1984) Once more on the comparison of growth in fish and invertebrates. *Fishbyte* **2**: 21.

Ricker, W. E. (1973) Linear regressions in fishery research. *J. Fish. Res. Board Can.* **30**: 409–34.

Roff, D. A. (1984) The evolution of life history parameters in teleosts. *Can. J. Fish. Aquat. Sci.* **41**: 989–1000.

Roff, D. A. (1986) Predicting body size with life history models. *Bioscience* **36**: 316–23.