

# Beverton and Holt's insights into life history theory: influence, application and future use

Simon Jennings<sup>1</sup> and Nick K. Dulvy<sup>1</sup>

**ABSTRACT:** The growth, maturity and mortality data needed to parameterize fish population models are often hard to obtain, and this led Beverton and Holt to explore simpler approaches for predicting key life history parameters and for dealing with multiple interrelated parameters in population dynamic equations. Their explorations led to the identification of dimensionless ratios among life history parameters, dubbed life history invariants, and provided insight into the trade-offs between growth, survival and reproduction. This work not only solved some parameterization issues, but laid the foundations for a dynamic research field encompassing major theoretical developments such as optimality theory and the analysis of energy allocation. Here, we review the influence of Beverton and Holt's studies of life histories in theoretical and applied ecology and show that their work continues to influence contemporary science. Little of their insight has been overturned by 50 years of subsequent research. Rather, that research has built on their insight to develop a more complete body of theoretical knowledge that links understanding of life histories, population dynamics, community assembly and ecosystem processes. Their work continues to be relevant to a number of challenges in theoretical and applied ecology. These include the development of models to predict invariants and scaling relationships, understanding macro-ecological patterns, assessing population and community responses to exploitation, and the development of tools to support an ecosystem approach to fisheries.

**Keywords:** allocation, conservation, fisheries, invariants, life history, macroecology, trade-offs.

## INTRODUCTION

Relationships between theoretical and applied ecology can be uneasy, with applied ecologists frustrated by the direction of theoretical research and theoreticians berating applied ecologists for not developing and applying their ideas. In this context, Beverton and Holt's investigations of life history theory were remarkable for two reasons. First, applied science drove the investigation of patterns that theoretical ecologists would subsequently try to explain. Second, Beverton and Holt's attitudes to cross-disciplinary research initiated a long-standing interaction between theoretical and applied ecology that is still active and relevant today. Indeed, they were among the first to recognize that the numerous comprehensive studies of exploited fish populations from the world's lakes, seas and oceans provided an ideal source of data for exploring general patterns in life history theory and population dynamics. The collation and analysis of such data would become common and influential in subsequent years (e.g. Pauly, 1978, 1980; Myers *et al.*, 1995; Froese and Pauly, 2006).

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<sup>1</sup> S. Jennings ([simon.jennings@cefas.co.uk](mailto:simon.jennings@cefas.co.uk)) and N. K. Dulvy: Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK

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By the late 1950s, Beverton and Holt had addressed many of the key problems in population analysis and developed methods to predict the potential yield from fish populations. The influence of their ideas is still apparent today (e.g. Quinn and Deriso, 1999). Following the publication of their treatise on the dynamics of fish populations (Beverton and Holt, 1957), Holt (1958), Beverton and Holt (1959) and Beverton (1963) considered numerous rearrangements of their fundamental yield equation, noting that dimensionless ratios between parameters could be substituted for the parameters themselves. These dimensionless ratios could be identified because many of the parameters appearing in the yield equations had units of time ( $t$ ) or  $t^{-1}$ .

Dimensionless ratios were almost constant within species or higher taxa whereas the individual life history parameters were more variable. Beverton and Holt described a number of dimensionless ratios among life history parameters, latterly dubbed life history invariants, and provided insights into the trade-offs between growth, survival and reproduction throughout an individual's lifespan. Their work not only solved some parameterization issues, but laid the foundations for a dynamic research field encompassing major theoretical developments such as optimality theory and energy allocation, parts of which are now manifest as modern life history theory and the metabolic theory of ecology (Roff, 1984, 1991, 1992, 2002; Charnov, 1993; Charnov *et al.*, 2001; Brown *et al.*, 2004; Charnov and Gillooly, 2004).

Here, we consider the origins and significance of Beverton and Holt's work on life histories, and how others have built on their insight to develop a more complete body of theoretical knowledge that links understanding of life histories, population dynamics, community assembly and ecosystem processes. We show that their work is still relevant to understanding macroecological patterns, species and community responses to exploitation and to the development of tools to support an ecosystem approach to fisheries.

## CHALLENGES IN FISH POPULATION ANALYSIS

In the Beverton and Holt (1957) yield equation, the response of a population to fishing mortality on a per-recruit basis depended on natural mortality ( $M$ ), fishing mortality ( $F$ ), growth rate ( $K$ , the Brody growth coefficient in the von Bertalanffy growth equation) and the age ( $t_c$ ) at first capture. These parameters appeared separately in the equation and they were difficult to estimate independently. In particular, scientists had long recognized the challenge of partitioning total mortality ( $Z$ ) into  $M$  and fishing mortality ( $F$ ). Even in the very intensively studied North Sea fisheries, there were serious difficulties with estimating  $M$ , as the 61 pages on different methods for estimating  $M$  in Beverton and Holt (1957) demonstrate. These were never resolved, and more than 20 years later John Pope's best estimate of  $M=0.2$  for North Sea cod and haddock was derived by cunning graphical manipulation of  $M=?$ , which proved to be no worse than estimates derived from incredibly data-intensive multispecies virtual population analyses!

Holt (1958) rearranged the Beverton and Holt (1957) yield equation to show that the potential yield per recruit ( $Y/R$ ) was, when expressed as a fraction of asymptotic weight ( $W_\infty$ , from the von Bertalanffy growth equation), a simple function of the ratio of growth rate to natural mortality rate ( $K/M$ ) and the age at recruitment. Beverton (1963) developed these ideas further, for the special case where fisheries targeted only adult fish, when the length at maturity ( $L_a$ ) and length at first capture ( $L_c$ ) would be equal. This was typically the case in a number of clupeid and engraulid fisheries. Thus, for an exploitation rate ( $E$ ) defined as  $F/(F+M)$ :

$$\frac{Y}{R} W_{\infty} = E \sum_{n=0}^3 \frac{U_n (1 - L_c / L_{\infty})^n}{1 + \frac{nK}{M} (1 - E)}, \quad (1)$$

where the summation term expresses the cubic relationship between length and weight with  $U_n = -1, -3, +3, -1$  for  $n = 0, 1, 2$  and  $3$ , respectively.

Although four parameters were required to apply equation (1) to an exploited stock, the essential aspects of a stock's response to fishing were captured in the ratios  $K/M$ , or its reciprocal, and  $L_c / L_{\infty}$ . The first ratio reflects intrinsic biological features of the population while the latter can be manipulated by fishery managers. Beverton (1963) summarized available information on  $M$  and  $K$  for clupeid and engraulid fish, and used analyses of populations within species, and among species, to show that the value of  $M/K$  was typically 1–2, even though lifespans varied by more than an order of magnitude.

When estimates of  $M$  were not available, Beverton (1963) investigated the use of the reciprocal of maximum age ( $1/T_{\max}$ ) as an index of  $M$ ; though perhaps this was a more applicable shortcut in the days when "historical" data on unexploited age structures were available. Beverton noted that the proportional relationship between the reciprocal of maximum age and  $K$  meant that the same fraction of the potential span of growth had been completed when the maximum lifespan was reached, regardless of whether the lifespan was short or long. He used the von Bertalanffy growth equation to show that 93–99% of the potential span of growth in length was completed within the maximum observed duration of life; even though lifespan ranged from 2 to 23 years! These relationships further suggested that the product  $KT_{\max}$  was an acceptable alternative to  $K/M$ . Hoenig (1983) later substantiated the value of the relationship between  $M$  and  $1/T_{\max}$  for 134 stocks from 79 species.

In the discussion of their 1963 paper, Beverton and Holt speculated on the adaptive interpretation of the relationship between growth and longevity, and suggested that it was advantageous to complete as much of the potential growth as possible within the lifespan, to maximize reproductive contribution to future generations. Although the immediate aim of their work on life histories was practical, they had ventured into areas now recognized as key parts of life history theory. Strangely, interest in the applied aspects of their work waned in subsequent years owing to the growing focus on predicting short-term yield based on pre-recruit surveys, but interest in their theoretical work on life history analysis was considerable (Charnov, 1993). In particular, theoretical ecologists began to consider the evolutionary mechanisms that would lead to the trade-offs they had observed.

## THE LIFE HISTORY INVARIANTS

In addition to the  $M/K$  ratio, Beverton and Holt identified a number of other dimensionless ratios including those between  $L_{\alpha}$  and  $L_{\infty}$  and between the age at maturity  $t_{\alpha}$  and  $M$  (also expressed as a relationship between  $t_{\alpha}$  and  $t_{\max}$ ). Reported values are typically in the range 1–2 for  $M/K$  (Beverton and Holt, 1959; Beverton, 1963; Charnov, 1993; Jensen, 1996), although some values <1 have been reported for both teleosts and elasmobranchs (Charnov, 1993; Frisk *et al.*, 2001) and there has been interest in the variation of values of invariants as well as in their consistency (e.g. Mangel, 1996). For  $L_{\alpha} / L_{\infty}$ , values are typically 0.4–0.9 (Beverton, 1992), and Charnov (1993) and Jensen (1997) reported values of 2 and 1.65, respectively, for  $t_{\alpha} M$ . More recently, Allsop and West (2003) suggested that the size at which animals change sex as a proportion of maximum size may also be

an invariant, though this prediction is largely a consequence of invariance in  $t_{\alpha} M$  and  $M/K$  (Gardner *et al.*, 2005).

## NO FREE LUNCH FOR THE DARWINIAN DEMON

The Darwinian demon is a hypothetical organism, imagined by Richard Law (1979), in which all the problems of maximizing reproductive output had been solved. The Darwinian demon began reproducing immediately after birth and produced large numbers of offspring continuously as it became older. Of course, as Law pointed out, no such animal exists because there is "no free lunch"; as investment in one aspect of life history is traded against another.

Charnov sought to examine Beverton's proposition that cross-species relationships between life history parameters reflected the Darwinian maximization of an individual's fitness, subject to trade-offs. These relationships were originally known as the Beverton–Holt dimensionless ratios, and in more recent literature they are often referred to as Charnov life history invariants, because he reawakened the wider evolutionary ecology community to the existence of the Beverton–Holt dimensionless ratios. Charnov asked whether the constancy or invariance of the Beverton–Holt ratios might emerge from evolutionary theory, given that the combination of life histories will be optimized to maximize fitness for the current environment. Charnov (1993) searched for the evolutionary equilibrium where fitness is maximized using a simple life history model based on three assumptions:

- that net lifetime reproductive rate ( $R_0$ ) is an appropriate measure of fitness. Net reproductive rate of the population is the average lifetime reproductive success multiplied by the survival probability;  $R_0 = S(\alpha)V(\alpha)$ , where  $S(\alpha)$  is the chance of living to the age at maturity ( $t_{\alpha}$ ) and  $V(\alpha)$  the number of daughters produced over a female's lifespan;
- that the lifetime reproductive success of a mature female is a power function of body size at maturity,  $V(\alpha) = L_{\alpha}^p$ , where  $L_{\alpha}$  is the length at maturity;
- that there is a trade-off between growth ( $K$ ) and maximum body size ( $L_{\infty}$ ) defined by the parameter  $h - L_{\infty} \propto K^{-h}$ , such that fast-growing species grow to a small maximum size and slow-growing species can attain a large maximum body size. This pattern of growth is widely observed in species with indeterminate growth, such as fish, urchins, shrimps, snakes or lizards, and can be described by the von Bertalanffy growth equation.

When fitness was maximized under these three assumptions, Charnov revealed two of the Beverton–Holt invariants. The first equation emerging from this fitness-maximizing evolutionary framework revealed a relationship between the strength of the trade-off between growth and body size,  $h$ , and the Beverton–Holt dimensionless ratio of the length at first maturity and maximum or asymptotic length  $L_{\alpha} / L_{\infty}$ :

$$h = \frac{L_{\alpha} / L_{\infty} - 1}{L_{\alpha} / L_{\infty}} \log_e (1 - L_{\alpha} / L_{\infty}). \quad (2)$$

The second equation showed a link between the exponent ( $p$ ) of the relationship between size at maturity and lifetime reproductive success and two of the Beverton–Holt dimensionless ratios  $L_{\alpha} / L_{\infty}$  and  $M/K$ :

$$p = \frac{L_\alpha / L_\infty}{1 - L_\alpha / L_\infty} \frac{M}{K} \quad (3)$$

Thus, the shape functions determining the strength of the relationships between growth rate and maximum body size ( $h$ ) and between size at maturity and lifetime reproductive success ( $p$ ) fix the value of the  $K/M$  and  $L_\alpha / L_\infty$  ratios. Charnov noted that intercepts do not appear in these solutions, which implies that the predicted values of  $L_\alpha / L_\infty$  and  $M/K$  are invariant to alterations in the intercept. Species with the same trade-off between growth rate and maximum body size ( $h$ ) and between size at maturity and lifetime reproductive success must have the same  $L_\alpha / L_\infty$  and  $M/K$ . Multiplying both equations together yields the third Beverton-Holt dimensionless ratio:

$$ph = \frac{-M}{K} K t_\alpha \quad \text{or} \quad ph = t_\alpha M \quad \text{or} \quad M = \frac{1}{t_\alpha} ph, \quad (4)$$

suggesting that the adult mortality rate is inversely related to the age at maturity in proportion to  $ph$ .

The optimality analysis of Charnov supports Beverton's original hypothesis that the dimensionless ratios observed across populations and species have arisen from natural selection to maximize an individual's fitness. Trade-offs and the diversity of life histories that have evolved help to maximize fitness under a range of environmental and evolutionary constraints. It is the common features of the trade-offs that lead to the invariants (Law, 1979). In particular, there is an implication that variation in an individual's growth performance influences the maximum body size attained, and the rate of natural mortality.

More recently, there have been substantial theoretical advances in the analysis of invariants, explaining why the Beverton and Holt invariants and others exist, and using these advances to explain the scaling of, for example, adult mortality and body size. Charnov *et al.* (2001), for example, developed a model based on evolutionary life history theory to predict the values of the life history invariants  $t_\alpha M$ , the product of the proportion of body mass given to reproduction per year and lifespan and the product of the maintenance metabolic rate per existing cell, divided by the cost of building a new cell and  $M$ . Reproductive investment had been largely overlooked in previous work, with egg numbers, offspring size and survival to maturation all subsumed within  $R_0$ .

## REPRODUCTIVE OUTPUT

Further investigations by Beverton nicely demonstrated how life history trade-offs served to maintain fitness across a range of environments. Beverton (1987) calculated the lifetime cohort egg production of walleye in lakes from California to northern Canada. The maximum ages of the walleye (*Sander vitreus vitreus*) ranged from 3 in the south to 20 in the north, and  $K$  varied from 0.05 in the north to 1.1 in the south. There was a very strong relationship between  $t_{\max}$  and temperature, which led Beverton to conclude that temperature, acting on growth, was forcing the rate of living and dying, an idea we will return to later. However, the invariant was relatively stable across the range of temperatures. Despite the very large differences in life histories, lifetime cohort egg production, a measure of reproductive fitness, was almost constant across all temperatures, suggesting that trade-offs between growth, maturity and longevity were sufficient

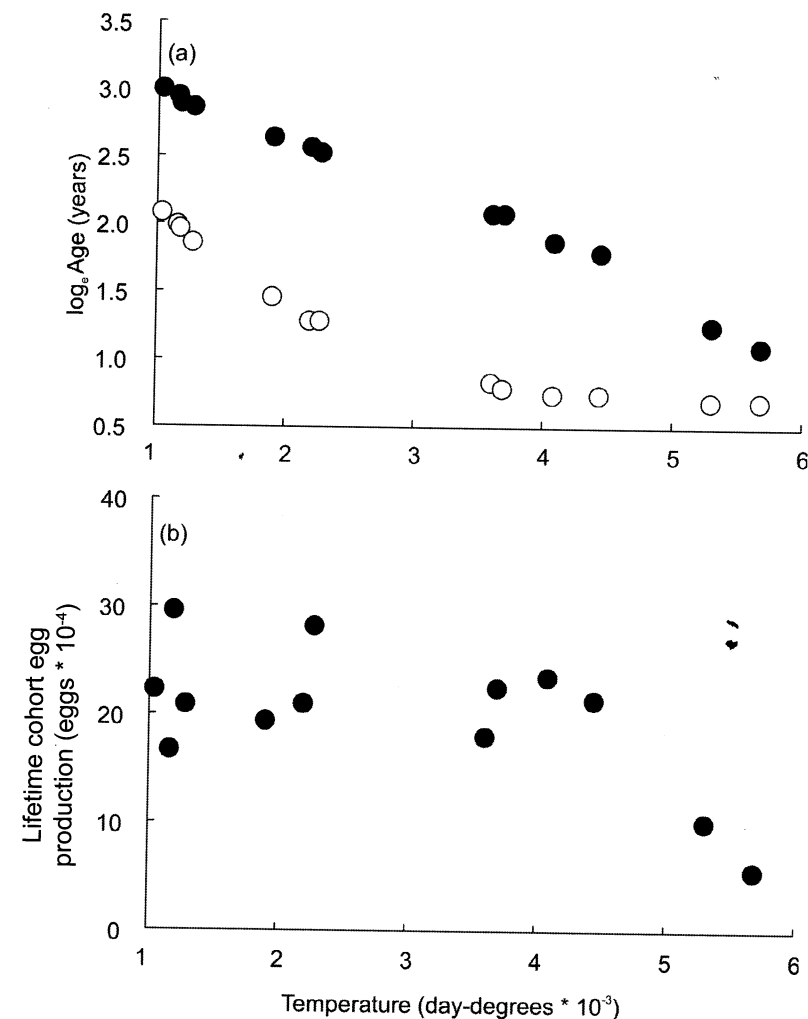


Figure 1. (a) Relationship between  $\log_e$  age at maturity ( $t_\alpha$ , open circles) or maximum age ( $t_{\max}$ , closed circles) and temperature (measured as day-degrees above 5°C, where 5°C is the minimum temperature for growth) for 13 walleye populations, and (b) the relationship between lifetime cohort egg production and temperature for the same populations.

to maintain fitness across most of the range of the species. Only at the very highest temperatures did lifetime cohort egg production decline, suggesting that the populations were physiologically unable to adapt to the forcing effects of extreme temperatures (Figure 1). Subsequently, Jennings and Beverton (1991) described a comparable pattern in Atlantic herring (*Clupea harengus*) populations living at different temperatures. Although lifetime reproductive output (measured as the product of egg size and fecundity) was not related to temperature, despite  $t_{\max}$  varying from 9 to 18.5 years, the age at maturity decreased and annual reproductive output increased with temperature. Both sets of results were consistent with Charnov and Berrigan's (1991) theoretical analyses in which they derived relationships between  $L_\alpha / L_\infty$  and  $K/M$  by assuming that natural

selection maximizes  $R_0$ , because in all cases the observed trade-offs served to maintain  $R_0$ . Moreover, the product of the proportion of body mass given to reproduction per year and lifespan, although variable, was not consistently related to temperature. In the case of the Beverton (1987) dataset (excluding the population at the highest temperature), there was a twofold variation in the product of the proportion of body mass allocated to reproduction per year and lifespan, but a 5.7-fold variation in lifespan.

## LIFE HISTORY TRADE-OFFS AND REPRODUCTIVE RATES

The existence of invariants suggests that evolution is governed by some very general features of life history trade-offs. The invariants now form part of a much wider understanding of such trade-offs, which link body growth, size and age at maturity, maximum body size and age, population growth, density-dependence and mortality. Therefore, life history trade-offs are not only informative about potential yields per recruit, but also about resilience to recruitment-overfishing and rates of recovery from low population size.

The intrinsic rate of natural increase is the maximum rate of population growth in the absence of density-dependence. In theory, the maximum rate of population growth should be when population sizes are smallest, but in practice this may not be the case because of the effects of depensation (Liermann and Hilborn, 2001). Density-dependence reduces the rates of population growth. The strength of density-dependence, typically known as compensation in the context of the spawner–recruit relationships used in fisheries, determines how the production of recruits per spawner changes with the abundance of spawners and the ability of populations to compensate for increased mortality.

Interest in the links between the intrinsic rates of increase and other life history parameters built on the theoretical work of Myers *et al.* (1997a), who developed a method for estimating the intrinsic rate of increase from widely available spawner–recruit data. The intrinsic rate of increase had formerly been calculated from the Euler–Lotka equation (e.g. Hutchings and Myers, 1994). However, the method was particularly data intensive and could only be applied to the relatively few populations where age-specific survival and fecundity schedules were available. The Myers *et al.* (1997a) method calculated the intrinsic rate of population increase from the slope of the spawner–recruit relationship at low spawner abundance, and expressed this rate as the number of spawners produced by each spawner per year ( $\hat{\alpha}$ ). The development of this method meant that intrinsic rates could be calculated for many more populations, and enabled Denney *et al.* (2002) to investigate relationships between intrinsic rates and other life history parameters. They showed that slow-growing species with large maximum body sizes had lower intrinsic rates of increase. Metabolic theory predicts that the relationship between body mass and the intrinsic rate of increase should scale with body mass as approximately  $W^{-1/4}$  (Savage *et al.*, 2004). The observed body mass scaling across 63 populations of exploited European marine fish described in Denney *et al.* (2002) was  $W^{-0.308}$ , not significantly different from the 0.25 scaling predicted from theory ( $p < 0.05$ ; Maxwell and Jennings, 2005). The resilience and potential recovery rate of populations is directly related to the intrinsic rate of population increase (Myers *et al.*, 1997a, 1999; Hutchings, 2002; Roff, 2002; Hutchings and Reynolds, 2004).

Life history variation can now be linked to the strength of compensation as well as to the intrinsic rate of increase. Large-bodied species (with slow growth, low natural mortality and late maturation) have higher fecundity, which results in greater scope for

density-dependent mortality at the planktonic stage (Rose *et al.*, 2001; Myers, 2002). This is broadly supported by an analysis of compensation in European fish stocks, where large-bodied species with low intrinsic rate of population increase show the greatest compensation (Goodwin *et al.*, 2006). Conversely, species with small body size (fast growth, early maturation) and high intrinsic rates of population increase exhibited weak compensation. This is consistent with life history theory in that small-bodied species are largely plankton-feeding clupeids (e.g. sprat, *Sprattus sprattus*, and herring) and the survival of recruits is determined largely by processes related to environmental variability; a density-independent process.

## POPULATION DYNAMICS

The observation that trade-offs serve to maximize reproductive output in the face of temperature-driven constraints on growth explains why species with different longevity and body sizes show predictable patterns in their population dynamics. One consequence of the invariance of  $M/K$  is that there is a predictable trade-off between the gain in mass of a cohort through body growth and the decline in numbers in that cohort through mortality. In the context of Beverton's (1987) study of lifetime reproductive output in the walleye and the knowledge that  $L_\alpha / L_\infty$  (or  $W_\alpha / W_\infty$ ) is fixed, it is not surprising that Holt (1958) had previously identified a relationship between  $M/K$  and the body size at which a cohort reaches maximum biomass while seeking to identify the size at first capture ( $L_c$  or  $W_c$ ) at which infinite  $F$  would provide the greatest possible yield per recruit from a fishery. This relationship was

$$W_{mb} = W_\infty [K / (K + M/3)]^3, \quad (5)$$

where  $W_{mb}$  is the weight of an individual when the cohort biomass is maximum (the minus sign shown in the original paper is a typographic error).

Dividing the bracketed terms in equation (5) by  $K$  allows  $W_{mb}$  to be expressed as a function of the  $M/K$  ratio:

$$W_{mb} = W_\infty [1 / (1 + M/3K)]^3. \quad (6)$$

If we assume a typical  $M/K$  value of 1.5 (e.g. Beverton, 1963; Charnov, 1993), then  $W_{mb} = W_\infty (2/3)^3$  and  $V_{mb} \approx 0.30W_\infty$ . Therefore, at equilibrium,  $W_{mb}$  occurs at a similar proportion of  $W_\infty$  in different species, even though the time at which the cohort reaches maximum biomass will vary by many years among species, owing to the effects of  $K$  and  $M$  (Figure 2).

More recently, the approach taken by Holt (1958) has been influential in providing the basis for developing a method to assess the size at which a cohort requires the maximum amount of energy to sustain its production ( $W_{me}$ ). Jennings *et al.* (2007) built on the approach of Holt (1958) to show that  $W_{me}$  for a population at equilibrium can be determined solely from knowledge of  $W_\infty$ , the slope of a relationship between log body size and trophic level ( $b$ ), the  $M/K$  ratio and transfer efficiency ( $\epsilon$ ):

$$W_{me} = W_\infty \left[ 1 / \left( 1 + \frac{M}{3K [0.75 - b(\log_e \epsilon)(\log_{10} e)]} \right) \right]^3. \quad (7)$$

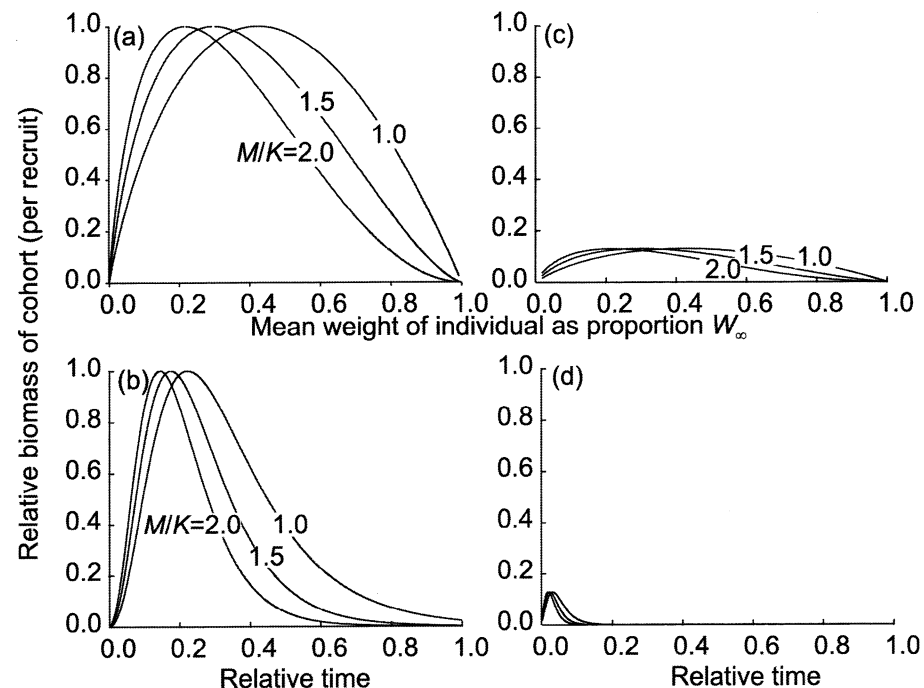


Figure 2. Evolution of cohort biomass as a function of the weight of an individual and as a function of time for a population, with (a, b)  $K = 0.1$  and  $W_{\infty} = 1000$  g, and (c, d)  $K = 0.6$  and  $W_{\infty} = 10000$  g, with values of the  $M/K$  ratio of 1.0, 1.5 and 2.0.

Figure 3 shows how  $W_{me}$ , expressed as a proportion of asymptotic weight, changes as a function of  $M/K$  and  $b$ . The practical value of this equation is in predicting how the energy requirements of a population vary with life history and feeding strategy, with consequent effects on competitive and predatory interactions in the community.

### THE ROLE OF METABOLISM IN SHAPING LIFE HISTORIES

We touched on temperature effects earlier, and here we elaborate on how life histories are influenced by the underlying effects of temperature on metabolic rate. Beverton and Holt (1959) speculated on the links between metabolic rate and  $K$ , based on experimental measurements of oxygen consumption in fish species that had also been the subject of population analysis. Subsequently, Beverton (1987) concluded that temperature was the "forcing factor" that determined the rate of living and dying, and that life histories would evolve around this constraint to maximize reproductive output.

The evolution of size has metabolic consequences, because metabolic rate is approximately proportional to  $W^{0.75}$ . Consequently, large-bodied animals expend less energy on maintenance metabolism, leaving relatively more energy available for growth (and reproduction) (Kleiber, 1932, 1947; Peters, 1983; West *et al.*, 1997; Gillooly *et al.*, 2001). There is still active debate about the theoretical basis for the approximate  $W^{0.75}$  scaling and the extent to which it is universal (Glazier, 2005; van der Meer, 2006), and

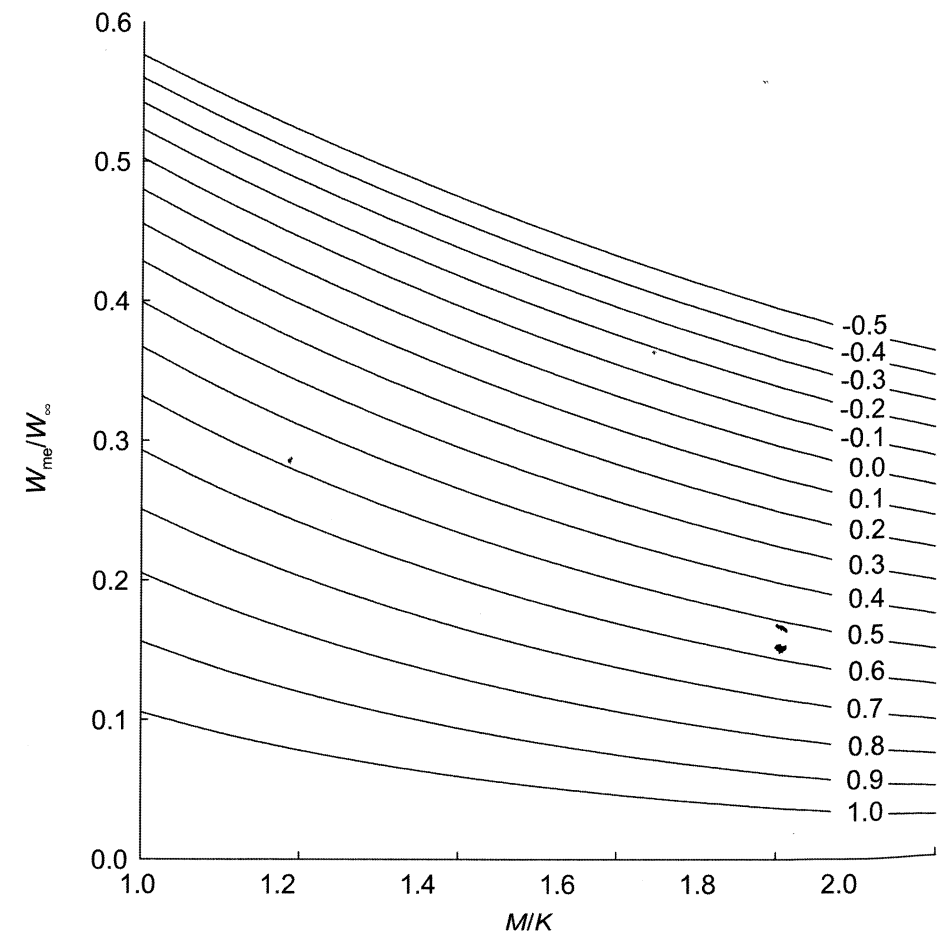


Figure 3. Relationship between  $W_{me}$ , expressed as a proportion of asymptotic weight  $W_{\infty}$  and  $M/K$  for different values of  $b$ , where  $b$  is the slope of the relationship between the log of body mass and trophic level.

different theoretical arguments suggest that scaling both within and among species can vary from  $W^{0.66}$  to  $W^1$  (van der Meer, 2006). Empirical data show that a wider range of values is possible, and although  $W^{0.75}$  may be an adequate approximation, simple physical laws that do not take account of physiochemical and ecological constraints are unlikely to provide accurate estimates. The intercepts of intraspecific  $W$  vs. metabolic rate relationships also vary considerably among species, reflecting the biology of the species concerned. For example, a fast-swimming pelagic species will have a much higher metabolic rate at a given size than a sedentary flatfish (e.g. Clarke and Johnston, 1999).

Temperature also has a direct effect on metabolic rate. When metabolic rate is mass-corrected, Clarke and Johnston (1999) showed that the cross-species relationship between temperature ( $T$  in Kelvin  $\times 10^3$ ) and resting metabolism ( $R_b$  as mmol oxygen gas  $h^{-1}$ ) for 69 species of fish was  $\log_e R_b = 15.7 - 5.02T^{-1}$ . In practice, this means that a tropical fish at  $30^\circ C$  has approximately six times the resting metabolic rate of a polar fish at  $0^\circ C$ , providing evidence for the forcing effect of temperature on metabolism. Within the physiological limits that are defined by evolution and determine the extremes of a species' range,



higher temperatures will therefore increase the energetic demands of individuals and populations at a given size and mean that they have to acquire more energy, with the associated risks of greater mortality (Pörtner and Knust, 2007). The role of temperature in forcing the rate of living and dying, and therefore in constraining life history trade-offs as predicted by Beverton and Holt (1959), was further demonstrated by Gillooly *et al.* (2001), who made the observation that the amount of energy per unit mass used over the average lifespan of an individual is approximately constant, regardless of body size and temperature. Charnov and Gillooly (2004) further demonstrated that temperature effects could account for changes in maturation, mortality and reproductive effort via life history optimization.

## PHYLOGENY AND MEASURING DIMENSIONLESS RATIOS

The process of natural selection in response to recent environmental and ecological conditions should result in life histories optimized for maximum fitness. However, history is important; species are defined by their shared evolutionary history as well as their current environment, and a considerable amount of life history variation can be explained by phylogeny (Freckleton *et al.*, 2002).

Beverton and Holt were careful to compare history traits among populations within each family of cod, herring, flatfish and redfish (Sebastidae). The assumption that differences among populations and species are solely attributable to local adaptation becomes less valid when seeking general rules applicable across a wider taxonomic range of species and families. The solution to this problem is to plot differences in life history traits between pairs of closely related taxa (populations, species, families etc.) rather than absolute values (Felsenstein, 1985; Harvey and Pagel, 1991). These differences or paired contrasts control for the autocorrelation resulting from shared evolutionary history. Hence, the observed contrasts result from adaptation to local conditions, because the taxa split and diverged from a common ancestor. The degree of difference between sister taxa depends, *inter alia*, on the time of divergence from the ancestor. The intraspecific and interspecific comparisons used by Beverton and Holt, as well as by later authors, were therefore a subset of a more general approach for controlling for evolutionary history and relatedness.

Controlling for evolutionary history is expected to be important when dealing with the diverse array of taxa now used for comparative analysis, although there are few empirical comparisons of controlled and non-controlled analyses. Ideally, controlling for phylogeny requires a molecular phylogenetic tree with estimates of the evolutionary distance between taxa. Although some information on tree shape may be available, more often than not estimates of evolutionary distance (branch lengths) are largely absent for more than a handful of species. Incorporating any form of phylogenetic knowledge can only improve the nesting of the variance and therefore confidence in the generality of the findings (Harvey and Pagel, 1991). The most accessible sources of phylogenetic knowledge for fish are the comprehensive taxonomies of Nelson (1994) or Eschmeyer (1998). These can be used as a backbone, with the relationships within families provided by morphological and molecular trees.

One might question whether controlling for phylogeny matters. For a narrow taxonomic array of populations within a species, it will probably matter less than when searching for greater generality using a more diverse array of taxa, although to some extent potential problems may be ameliorated if many taxa are well represented. Again, there are few empirical tests of the effects of not accounting for phylogeny on patterns such

as scaling relationships. However, there is some evidence that incorporating knowledge of evolutionary relationships can improve the probability of detecting expected patterns. This is well-illustrated by the apparent absence of a relationship between fecundity and recruitment variation of broadcast spawning fish. A relationship was theoretically expected (Mertz and Myers, 1994), but went undetected until phylogeny could be controlled for (Rickman *et al.*, 2000).

## APPLICATIONS

Analyses based on life history invariants and the relationships between life history parameters have a range of applications in fish population (and community) assessment, and recent theoretical developments provide a stimulus for further applications. There is still significant scope for interaction between theoretical and applied ecologists, and fisheries science will likely benefit from many recent developments in the understanding of life histories (e.g. Charnov *et al.*, 2001; Goodwin *et al.*, 2006). Relevant applications of theory include: (i) the better prediction of natural mortality rates in data-poor situations (e.g. when just body size and temperature data are available; Charnov and Gillooly, 2004); (ii) growth models for fish that have a stronger theoretical grounding than the widely used von Bertalanffy growth model (e.g. of the form  $dW/dt = aW^{0.75} - bW - cW$ , rather than  $dW/dt = aW^{0.66} - bW$ , where  $aW$  describes intake,  $bW$  maintenance, and  $cW$  reproductive costs; see West *et al.*, 2001, and Charnov and Gillooly, 2004); (iii) predicting vulnerability (Myers *et al.*, 1997a, 1997b, 1999; Jennings *et al.*, 1999; Dulvy and Reynolds, 2002; Dulvy *et al.*, 2004); (iv) using invariants to predict complex aspects of life history and to simplify population analyses (Pope *et al.*, 2000); and (v) predicting community responses to fishing (Pope *et al.*, 2006).

The existence of trade-offs in life histories has continued to stimulate applied research that built on the spirit of Beverton and Holt's original aim – to simplify the parameterization of population models (e.g. Pauly, 1980; Pope *et al.*, 2000). There have been several attempts to predict  $M$  from other aspects of the life history, either based on empirical relationships or directly on theory (Pauly, 1980; Hoenig, 1983; Peterson and Wroblewski, 1984; Lorenzen, 1996). Pauly (1980), for example, simply put a range of parameters that were expected to influence  $M$  into a multiple regression and sought the combinations of parameters that provided the best fit to data for 175 fish populations. The final (best fit) model included temperature as well as  $K$  (which is in part responsive to temperature). The use of the Pauly (1980) approach for estimating  $M$  has become so widespread that many of the values of  $M$  appearing in data compilations used to study the invariants have already been derived using methods based on the invariants. For this reason, it is important for analysts to check the original sources of data before embarking on their "new" analyses.

One disadvantage of the Pauly (1980) approach was its relatively loose relationship with theory. However, the theoretical basis of relationships between body size, mortality and temperature is increasingly well established (e.g. Charnov and Gillooly, 2004), and there is scope to take account of these developments in fishery science. Gillooly *et al.* (2001) and others (e.g. Clarke and Johnston, 1999; Brown *et al.*, 2004) use the van't Hoff-Arrhenius relationship to describe relationships between biological rates and temperature, and Savage *et al.* (2004) and Charnov and Gillooly (2004), for example, have temperature "corrected" Pauly's (1980) mortality data to establish a clear relationship between natural mortality and body mass (Figure 4). A relationship of this form can be

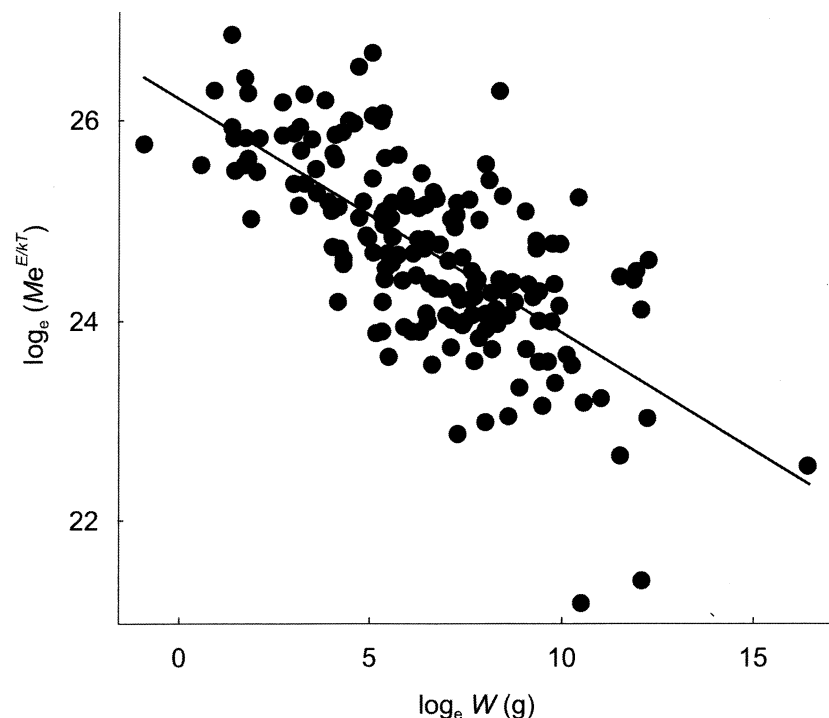


Figure 4. Relationship between temperature-corrected natural mortality rate ( $\log_e Me^{E/KT}$ ) and body mass based on the data compilation of Pauly (1980). Redrawn from Charnov and Gillooly (2004), with modification ( $M$  expressed as  $y^{-1}$ ).

rearranged easily to express  $M$  as a function of body size  $W$  and temperature. Therefore, the relationship derived by Charnov and Gillooly (2004) (Figure 4) leads to the following equation for  $M$ :

$$\log_e M = -0.24 \log_e W + 26.25 - E / kT, \quad (8)$$

where  $E$  is the activation energy of metabolism, which is reported to be 0.6–0.7 eV (Brown *et al.*, 2004),  $k$  is Boltzmann's constant ( $8.62 \times 10^{-5}$  eV Kelvin $^{-1}$ ), and  $T$  is the temperature in Kelvin ( $^{\circ}\text{C} + 273$ ). Note that the scaling relationship between mortality and body mass is  $W^{-0.24}$ , close to the value of  $W^{-0.25}$  predicted from theory.

Although the use of invariants in assessing population responses to exploitation was well recognized by Beverton and Holt, those assessments were based on "per recruit" analyses that did not account for the factors that served to sustain and modify recruitment. Subsequent investigation of the links between life histories, intrinsic rates of increase and density-dependence have shown that life histories also help to predict how and whether recruitment will respond to exploitation. Therefore, the identification of links between life history parameters and density-dependence (Goodwin *et al.*, 2006) has provided considerable insight into the boom and bust paradox of commercially important demersal stocks, e.g. Northwest Atlantic cod and North Sea cod (Myers *et al.*, 1996, 1997b; Horwood *et al.*, 2006). These stocks exhibited consistently high yields at early stages of exploitation,

followed by collapse and a persistent lack of recovery. Evolution of the yield is consistent with a high compensatory reserve at large population size coupled with a low intrinsic rate of population increase at low population size. By contrast, the productivity of small-bodied pelagic species may be attributable to their capacity to track the abundant energy at the base of the foodweb, and their relatively high intrinsic rate of population increase allows rapid recovery on cessation of fishing (Goodwin *et al.*, 2006).

## CONCLUSIONS

It is remarkable that attempts to solve practical problems in fisheries science have had such far-reaching ramifications in ecology. Although much of Beverton and Holt's insight has been built upon and refined, little has been overturned by 50 years of subsequent research. We believe that their ideas are still relevant and still useful, especially in understanding population and community-level processes and macroecological patterns, the responses of species and communities to exploitation and the development of tools to support an ecosystem approach to fisheries. In the last area, the use of Beverton and Holt dimensionless ratios to support simple approaches for addressing the complex dynamics of multiple populations provides real prospects for assessing species and community dynamics when the individual species will never be the subject of intense and focused study.

Some 50 years of progress in understanding the links between life histories, population dynamics, energy requirements and exploitation have highlighted the benefits to be gained from strong interactions between pure and applied ecology. Aspects of modern fishery science and theoretical ecology are often poorly related and we hope that the much-touted advent of an ecosystem approach to fisheries will once again encourage closer and more fruitful interaction.

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## The “soundscape” of the sea, underwater navigation, and why we should be listening more

A. John R. Cotter<sup>1</sup>

**ABSTRACT:** Sound is the best transmitted of all radiations underwater. Here I argue speculatively that the sea is filled heterogeneously with varying sounds forming an underwater “soundscape” that could be as familiar to marine animals as the visual landscape is to humans. High frequency sounds come naturally from wind, sediment transport and rainfall. Low frequency sounds come from surf, long-period waves, geological and meteorological processes, and probably from turbulence associated with currents. Biologically produced sounds tend to be intermittent. Man-made sounds can be loud and pervasive, e.g. shipping, sonar, seismic exploration, mineral extraction. Transmission pathways are bent by refraction, reflection, and diffraction, causing zones of high and low sound intensity, depending on locality, times and seasons. The zoning varies with frequency, leading to variable harmonic structures, the acoustic equivalent of colour. Marine life could use acoustic patterns to help them order their lives as well as to navigate during migrations. Passively listening to marine animals and the sounds they hear could tell us much about their biology, and could also have practical applications in fisheries science and management. We need to become more aware of noise pollution that could be interfering significantly with biological processes.

Keywords: fish, marine mammals, marine sound, migration, noise pollution in the sea, passive acoustics, underwater navigation.

### INTRODUCTION

Light is scarce in the sea other than in shallow, clear waters, yet the eyes of fish and other marine animals are well adapted in numerous ways to the visual conditions of their habitat (Warrant and Locket, 2004). Sound, on the other hand, is the best transmitted of all radiations underwater (Urlick, 1983). Low frequency sounds in particular, e.g. from underwater earthquakes, or explosions, can travel thousands of kilometres (Medwin and Clay, 1998), and underwater sound exists at all depths in a variety of frequencies, not just those audible by humans (20–20 000 cycles per second, Hertz, or Hz). We can confidently expect that fish and other marine organisms have evolved to benefit from the pervasive presence of sound in at least as many ways as they have to light.

Despite this, the study of sounds made and used by fish, i.e. passive acoustics, remains an academic branch of marine biology notwithstanding the extensive practical use made of echosounders and sonar, i.e. active acoustics, for finding fish and studying the physical environment. Our predilection for visually researching life in the sea probably stems from the beauty and fascinating appearances of marine life, from our own extreme reliance on sight, and from the fact that we seldom hear sounds originating underwater because of the effective acoustic barrier formed by the sea's surface. A practical reason is that

<sup>1</sup> A. J. R. Cotter (john.cotter@cefas.co.uk): Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK

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50 years on from Beverton and Holt



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