

The inverse life-history problem, size-dependent mortality and two extensions of results of Holt and Beverton

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Abstract

In 1958, Sidney Holt developed a model to determine the optimal mass at which to harvest a cohort of fish having von Bertalanffy growth and experiencing constant natural mortality. Holt and Ray Beverton then gave a life-history interpretation to the analysis, from which Beverton developed a theory of Growth, Maturity, and Longevity (GML) that allows one to predict quantities such as age at maturity or relative size at maturity using life-history parameters. I extend their results in two ways. First, keeping the original formulation, in which the rate of natural mortality is constant, I show how one can invert Beverton's result to determine the rate of natural mortality from life-history data. I illustrate this inverse method with data on three species of tuna and compare the estimates with those based on tagging. Second, I extend Beverton's GML theory to include size-dependent mortality. I explore previously published mortality models and introduce a new mortality function that has size-independent and size-dependent components. I show that the new size-dependent mortality function leads to the prediction that age at maturity depends upon asymptotic size (as well as the other life-history parameters), something that Beverton's original theory lacked. I illustrate this extension with a simple example, discuss directions for future work and conclude that nearly 60 years on these contributions of Holt and Beverton continue to lead us in new and exciting directions.

KEYWORDS

age at maturity, asymptotic size, Growth-Maturity-Longevity, rate of mortality, tuna, von Bertalanffy growth

In celebration of Sidney Holt receiving the Beverton Medal from the Fisheries Society of the British Isles, on the 50th Anniversary of the Society

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Etymology of Ghoti

George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.



1 | INTRODUCTION

Inferring life-history parameters and examining their impact on the dynamics of individuals, populations and communities are always going to be important goals in biology. Here, I extend an idea concerning computation of the optimal age for Yield Per Recruit (YPR) that Sidney Holt first published (Holt, 1958) and that Ray Beverton extended into a theory of Growth, Maturity, and Longevity (GML) (Beverton, 1987, 1992, 2002; Beverton & Holt, 1959) in two ways.

First, I show how Beverton's original theory, in which one assumes that the rate of natural mortality is constant, can be applied to the inverse life-history problem. That is, rather than asking "given the rate of natural mortality, von Bertalanffy growth rate and size fecundity exponent, what is the optimal age at maturity?" we ask "given the von Bertalanffy growth rate, size fecundity exponent and age at maturity, what is the rate of natural mortality?" Because in a sample of fish, each mature individual provides data for these life-history parameters, we are able to develop both point estimates and distributions for the rate of natural mortality, a parameter that is exceptionally hard to measure. I illustrate this inverse method by developing distributions for the rate of natural mortality for three species of tuna and compare these with estimates obtained by Hampton (1991, 2000) using tagging data.

Second, I show how to extend Beverton's GML theory when the rate of natural mortality depends upon size. Asymptotic size does not appear in Beverton's original theory (why this happens will be seen below). However, it is now generally agreed that mortality of fish is an explicit function of size (and thus an implicit function of age; e.g., Brodziak, Ianelli, Lorenzen, & Methot, 2011; Charnov, Gislason, & Pope, 2013; Gislason, Daan, Rice, & Pope, 2010; Gislason, Pope, Rice, & Daan, 2008; Lorenzen, 2000).

For example, Gislason et al. (2010) used an extensive statistical study conclude that the rate of mortality depends not only on size but on asymptotic size L_∞ and von Bertalanffy growth rate k according to (their Equation (2) exponentiated)

$$M_g(L) = e^{0.55} \cdot k \cdot L_\infty^{1.44} / L^{1.61} \quad (1)$$

Charnov et al. (2013) found that an equally good fit to the data is given by

$$M_c(L) = e^{-0.05} \cdot k \cdot \left(\frac{L_\infty}{L}\right)^{1.46}$$

and then argue that 1.46 and 0.05 in these equations are not statistically different from 1.5 and 0, respectively, to write

$$M_c(L) = k \cdot \left(\frac{L_\infty}{L}\right)^{1.5} \quad (2)$$

To reach Equation (2), Charnov et al. (2013) essentially refit three of the parameters in Gislason et al. (2010) (the numerical coefficient, which goes from $e^{0.55} = 1.73$ in Equation (1) to 1 in Equation (2), and the exponents which go from 1.44 and 1.61 in Equation (1) to 1.5 in Equation (2)).

I will offer an alternative model for the size dependence of mortality, with intuitive biological appeal and analytical advantages for predicting age at maturity. I show that with this model of size-dependent mortality, the optimal age of maturity depends upon asymptotic size, which does not occur in Beverton's original theory. I illustrate this dependence with a numerical example.

Both extensions require no more than elementary calculus, although further development of them (Appendix) becomes a bit more complicated.

To ensure that this note is self-contained, I first summarize what Holt and Beverton did and then derive the extensions and their implications. In the discussion, I first consider the inverse life-history problem, resolve some questions left open by the analyses of Gislason et al. (2010) and Charnov et al. (2013) and finally raise some new questions. I conclude that the original analysis of Holt—almost 60 years old—and the fuller GML theory of Beverton—now 25 years old—are still fertile areas for new directions in research.

2 | WHAT HOLT AND BEVERTON DID

Holt (1958) envisioned individuals in a cohort following a common von Bertalanffy growth curve; mass at age a is $W(a) = W_\infty(1 - e^{-ka})^3$ where W_∞ is the asymptotic mass and k is the von Bertalanffy growth constant (see Mangel, 2006 for a derivation). The full von Bertalanffy description of growth is $W(a) = W_\infty(1 - e^{-k(a-a_0)})^3$ where $a_0 < 0$ is the theoretical age at 0 size. When $W(0)$ is small, a_0 is often set equal to 0. In the von Bertalanffy formulation, the allometry between mass and length is strictly cubic, that is $W \propto L^3$. Furthermore, asymptotic size is not a fundamental parameter, but rather a combination of an anabolic parameter and the growth rate; see Charnov et al. (2013), Mangel (2006) and Section 5 for more details.

If the rate of natural mortality is a constant M , then the expected mass at age a of a cohort of initial size N_0 individuals is $N_0 e^{-Ma} W_\infty(1 - e^{-ka})^3$. Thus, for a specific cohort, survival is a declining function of age and mass is a saturating function of age, so that there is an age at which harvesting this cohort maximizes expected biomass, obtained by taking the derivative of the expected mass with respect to age and setting it equal to 0. Holt showed that at the optimal age for harvest, mass is:

$$W_{\text{opt}} = W_\infty \left(\frac{3}{3+M/k}\right)^3$$

One can think of this as the ultimate YPR analysis in which there is no fishing mortality until the age giving W_{opt} and then the fishing mortality is infinite.

Beverton and Holt (1959) gave a life-history interpretation to Holt's analysis and Beverton (1992, 2002) more fully developed it into a life-history theory of GML. I begin with a slight elaboration of Beverton's theory, in which we do not necessarily assume that reproduction is proportional to mass. Dick, Beyer, Mangel, and Ralston (2017) give an example of a genus—*Sebastes*—in which the length-fecundity exponent ranges from about 3.5 to more than 5.0.

We describe growth by the von Bertalanffy formula for length $L(a)$ at age a with $a_0 = 0$

$$L(a) = L_\infty(1 - e^{-ka}) \quad (3)$$

where L_∞ is asymptotic length and k is as before. We assume that natural mortality M , is independent of size and that lifetime reproduction for an individual who matures at size l is ϕl^b .

With these assumptions, the fitness $F(a|L_\infty, k, M, b, \phi)$ of an individual who matures at age a given the life-history parameters is

$$F(a|L_\infty, k, M, b, \phi) = e^{-Ma} \phi L(a)^b = e^{-Ma} \phi [L_\infty(1 - e^{-ka})]^b \quad (4)$$

We find the optimal age at maturity by elementary calculus (Mangel, 2006, p. 23 ff)

$$a_m = \frac{1}{k} \ln \left(\frac{M + bk}{M} \right) \quad (5)$$

Since ϕ and L_∞ are constants with respect to age in Equation (4), they divide out when the derivative is taken and set equal to 0. Typically, one uses this theory by specifying the life-history parameters and predicting age at maturity. This extremely simple theory often does remarkably well (e.g. Mangel & Abrahams, 2001).

An alternative approach to age at maturity is to make the "most plausible assumption" (Charnov et al., 2013, p. 217) that the age of maturity is the age at which the rate of change of mass is a maximum. Then simple calculus shows that $a_m = \log(3)/k$, but this approach cannot not consider the trade-offs in growth and mortality explicitly in determination of the age at maturity (see the Appendices in Charnov et al. (2013) for further discussion).

Finally, although it appears that these results apply only to a semelparous organism, if there is no growth after maturity and we interpret $F(a|L_\infty, k, M, b, \phi)$ as annual reproductive output, then since expected lifetime is $1/M$, expected lifetime reproduction is $\frac{F(a|L_\infty, k, M, b, \phi)}{M}$ and the optimization problem does not change at all. If there is substantial growth after maturity, then a different approach is needed (see Section 5).

3 | THE INVERSE LIFE-HISTORY PROBLEM

We can invert Equation (5) to solve for M to obtain a point estimate for the rate of natural mortality conditioned on the length-fecundity exponent, the von Bertalanffy growth rate and the age at maturity

$$\hat{M} = \frac{bk}{e^{ka_m} - 1} \quad (6)$$

If we have distributions for the other parameters, then we are able to construct an informative prior for M . For example, Dick et al. (2017) conducted a meta-analysis of the fecundity of the rockfish. Their result is a posterior-predictive distribution of the length-fecundity exponent b , so that drawing from this posterior-predictive distribution provides individual values of b , which can be complemented by individual values of k and a_m if those distributions are known. When they are not known, we can proceed by making assumptions about the distributions.

For example, to account for variation in k , where \hat{k} is the point estimate, one could assume that for the i th draw from the posterior-predictive value of b the associated value of growth rate, k_i is

$$\log(k_i) = \log(\hat{k}) - 0.5\sigma_k^2 + \sigma_k Z_i \quad (7)$$

where Z_i is a Normal(0,1) and σ_k is the standard deviation in growth rate.

To account for variation in age at maturity, one can use the maturity ogive

$$p_m(a) = \Pr\{\text{mature by age } a\} = \frac{1}{1 + \exp(a_{50} - a/\sigma_a)} \quad (8)$$

where a_{50} is the age at which half of the individuals in a cohort are mature and $\sigma_a = 0.5$ characterizes the dispersion of maturity around that age. For an individual draw of the length-fecundity exponent and growth rate, we then draw a uniform [0,1] random variable and compare that with the maturity ogive to determine the age at maturity on this draw.

To illustrate application of the inverse life-history method, I extracted data on skipjack tuna (*Katsuwonus pelamis*, Scombridae), yellowfin tuna (*Thunnus albacares*, Scombridae) and southern blue fin (*Thunnus maccoyii*, Scombridae) tuna from the global scombrid life-history data set (Juan-Jordá, Mosqueira, Friere, Ferrer-Jordá, & Dulvy, 2016). For these species:

1. There are data on average and variance in the von Bertalanffy growth rate k .
2. There are data for average age at maturity a_{50} . I assumed that $\sigma_a = 0.05a_{50}$.
3. There are data on average length-fecundity exponent for all three species and data on variance in the length fecundity exponent for skipjack and yellowfin tuna. For bluefin tuna, I followed the result of Dick et al. (2017) and assumed a normal distribution for b with Coefficient of Variation 12.5%.

Thus, we are able to generate an entire prior distribution for the rate of natural mortality, conditioned on the fecundity parameter, observed growth rate and age at maturity (Figure 1). The point estimate for skipjack tuna is $\hat{M} = 1.25$. For comparison, Hampton (2000)—using tagging data—estimated that M for the midsizes of skipjack tuna (41–51, 51–60 and 61–70 cm), which comprise the bulk of the exploited range, are 1.6, 1.2 and 2.0 year⁻¹, respectively. The distribution in Figure 1 includes all of those values. The point estimate for yellow fin tuna $\hat{M} = 0.93$ is a bit larger than that reported by Hampton (2000), who noted that $M = 0.8$ is most commonly used in assessment and for the size-classes 51–60, 61–70 and 71–80 cm the estimates for M are 0.68, 0.44 and 0.69. However, Hampton estimated $M \approx 1$ for the 41–45 cm size-class (see his figure 10) and values of M between 0.5 and 1.0 are highly probable using the inverse life-history method (Figure 1). The point estimate for southern bluefin tuna is $\hat{M} = 0.25$; for comparison Hampton (1991) suggested values of M between 0.24 and 0.28 year⁻¹ and the probability distribution in Figure 1 captures the entire range of values reported by Hampton.

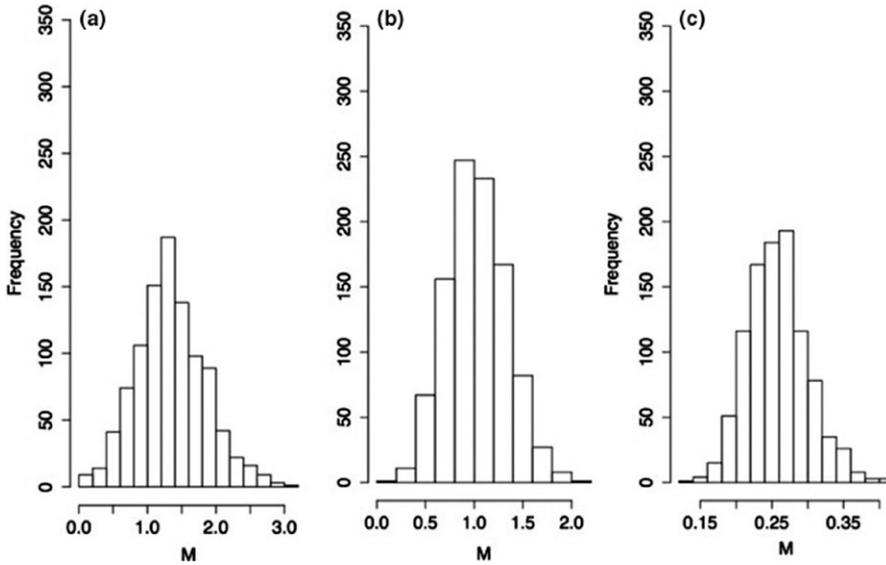


FIGURE 1 Probability distributions for the rate of mortality for skipjack tuna (a), yellowfin tuna (b) and southern blue fin tuna (c) using the inverse life-history method with Beverton's original Growth, Maturity, and Longevity theory. Point estimates for M are, respectively, 1.25, 0.93 and 0.25. See text for details and comparison with other published estimates

These results should be taken as illustrative, as some of the species are far from asymptotic size when at the age of maturity (see Section 5).

4 | INCORPORATING SIZE-DEPENDENT MORTALITY

4.1 | The form of size-dependent mortality

Rather than using either $M_g(L)$ or $M_c(L)$, I offer an alternative approach to size-dependent mortality. In particular, write

$$M(L) = m_0 + \frac{m_1}{L} \tag{9}$$

where m_0 and m_1 are parameters. If both parameters are both positive, we can interpret m_0 as the rate of size-independent mortality and m_1 as the rate of size-dependent mortality. If one of them is negative, then we lose such interpretation, but still have the interpretation that survival from age a to age $a + 1$ is $\exp(-m_0 - m_1/L(a))$, so that the requirement for biologically meaningful parameters is that $m_0 + \frac{m_1}{L} > 0$ for all values of L .

Snover, Watters, and Mangel (2006) used Equation (9) in the study of top-down and bottom-up control of life histories in coho salmon (*Oncorhynchus kisutch*, Salmonidae) and Carlson, Kottas, and Mangel (2010) developed a Bayesian method for estimating the m_0 and m_1 from only size distributions, with application to three-spined stickleback (*Gasterosteus aculeatus*, Gasterosteidae).

To compare Equation (1, 2 and 9), I took Equation (1) (the regression result of Gislason et al. (2010)) as the true state of nature and in Figure 2 show the predictions of Equation (1) (solid line), Equation (2) (red circles) and Equation (9) (blue crosses) for Pacific Ocean Perch (*Sebastes alutus*, Sebastidae) and Sqaurespot Rockfish (*Sebastes hopkinsi*, Sebastidae) where I determined the parameters m_0 and m_1 by matching in the rate of mortality at age 1 and at the age of maturity and used growth curves from Love, Yoklavich, Thorsteinson, and Butler (2002).

Survival to age a , $S(a)$, always satisfies the differential equation (Mangel, 2006; Hilborn and Mangel 1997)

$$\frac{dS}{da} = -M(L(a))S \tag{10}$$

when $M(L(a)) = M$, a constant, the solution of this differential equation with $S(0) = 1$ is $S(a) = e^{-Ma}$.

For the mortality model in Equation (9)

$$S(a) = \exp \left[-m_0 a - m_1 \int_0^a \frac{ds}{L(s)} \right] \tag{11}$$

One consequence of Equation (11) is that there is an infinite number of ways of getting the same survival to a specific age. For example,

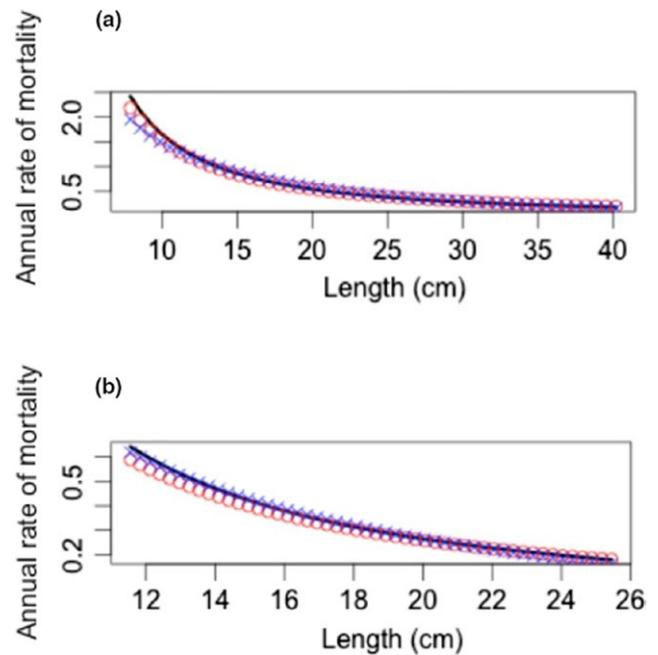


FIGURE 2 Comparison of the length-dependent mortality predicted by the regression of Gislason et al. (2010) (black line) with the approximation proposed by Charnov et al. (2013) (red circles) and the length-dependent form in Equation (9) (blue crosses) for Pacific Ocean Perch (a) and Sqaurespot Rockfish (b). [Colour figure can be viewed at wileyonlinelibrary.com]

if survival to age a_{\max} is $S(a_{\max})$, then with $m_1 = 0$ we obtain the maximum value for m_0 from $S(a_{\max}) = \exp(-m_{0,\max} a_{\max})$ and whenever $m_1 > 0$, the value of m_0 giving the same survival to age will be less than this maximum value. Indeed, there is a linear relationship between m_0 and m_1 , conditioned on the same survival to a_{\max} , determined by the value of the integral in Equation (11) (Snover et al., 2006; Figure 3).

4.2 | The implication of size-dependent mortality on predicting age at maturity

Suppressing the dependence on the life-history parameters, the generalization of Equation (4) is

$$F(a) = S(a)\phi L(a)^b \quad (12)$$

In the main text, I will focus on the analysis of Equation (12) with mortality given by Equation (9); in the Appendix, I discuss the situation when mortality is given by $M_g(L)$ or $M_c(L)$.

To find the optimal age of maturity, we differentiate Equation (12) with respect to a , using the product and chain rules of elementary calculus, and obtain

$$F'(a) = \frac{dS}{da} \phi L(a)^b + S(a) \phi b L(a)^{b-1} \frac{dL}{da} \quad (13)$$

$$= -M(L(a)) S(a) \phi L(a)^b + S(a) \phi b L(a)^{b-1} \frac{dL}{da} \quad (14)$$

substituting Equation (9) for $M(L(a))$ we obtain

$$F'(a) = S(a) \left(-m_0 - \frac{m_1}{L(a)} \right) \phi L(a)^b + S(a) \phi b L(a)^{b-1} \frac{dL}{da} \quad (15)$$

We set this derivative equal to 0 and simplify to obtain

$$m_0 L(a) + m_1 = b \frac{dL}{da} \quad (16)$$

Since $L(a) = L_\infty (1 - e^{-ka})$, one can directly verify that $\frac{dL}{da} = k L_\infty e^{-ka}$ (yet another way of characterizing von Bertalanffy growth) and Equation (16) becomes

$$m_0 L_\infty (1 - e^{-ka}) + m_1 = b L_\infty k e^{-ka} \quad (17)$$

which we solve for a_m

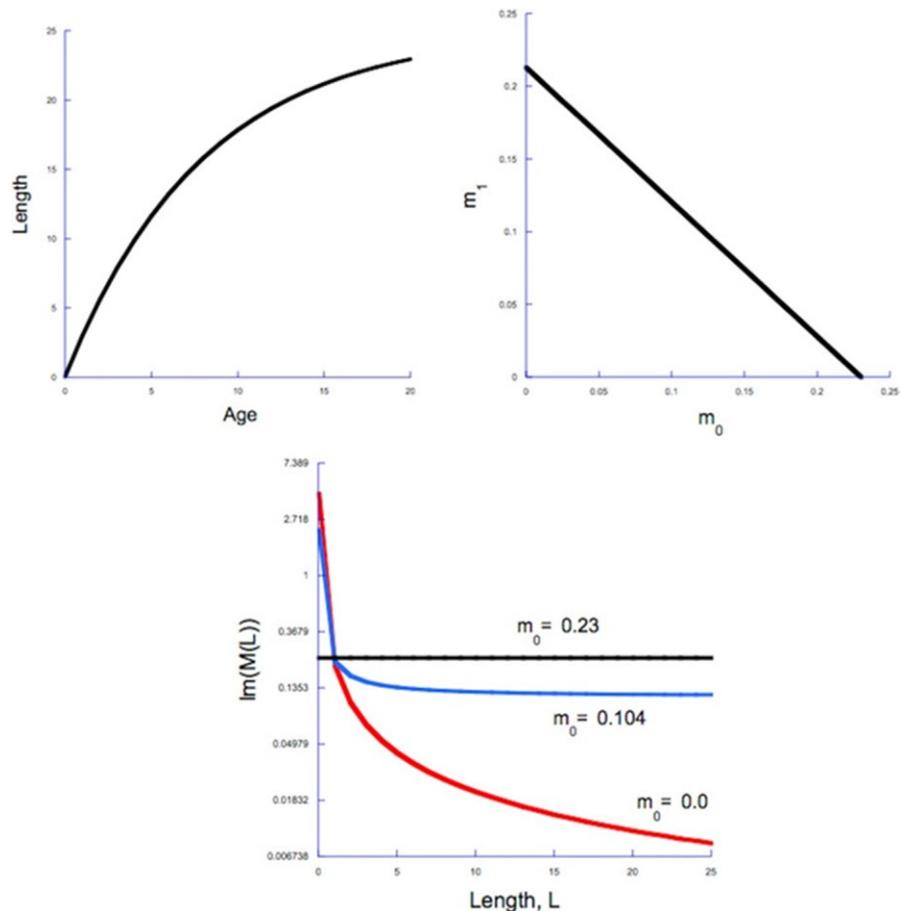
$$a_m = \frac{1}{k} \ln \left[\frac{(bk + m_0) L_\infty}{m_0 L_\infty + m_1} \right] \quad (18)$$

This is the second extension of the results of Holt and Beverton.

Equation (18), a prediction for the optimal age at maturity, now involves all five of the life-history parameters: asymptotic size, von Bertalanffy growth rate, length-fecundity exponent and the size-independent and size-dependent rates of mortality.

If we set $m_1 = 0$ then Equation (18) reduces to Equation (5) (with $M = m_0$), as it must. However, notice that if $m_0 L_\infty \gg m_1$, then Equation (18) also reduces to Equation (5). Thus, we conclude that the simpler expression holds not only when the rate of mortality is constant, but also when the condition $L_\infty \gg m_1/m_0$ holds.

FIGURE 3 Illustration of the effects of the size-dependent mortality model in Equation (9). I consider a fish growing according to a von Bertalanffy curve with initial size 0.01 cm, asymptotic size 25 cm and growth rate $k = 0.125$ per year (upper left-hand panel). When survival to age 20 is 0.01, there is a line of possible values of m_0 and m_1 giving the same survival to age (see Snover et al., 2006 for details); upper right-hand panel. Three examples of size-dependent mortality are shown in the lower panel. When $m_1 = 0$, the rate of mortality is independent of size; when $m_0 = 0$, the rate of mortality only depends upon size; for intermediate values of m_0 there is an initially strong dependence on size, but essentially size-independent mortality for larger sizes (ages). [Colour figure can be viewed at wileyonlinelibrary.com]



But otherwise, asymptotic size will enter into prediction of age at maturity. To illustrate the result, in Figure 4, I plot the predicted age at maturity for $k = 0.125$, $b = 3.5$ and $m_0 = 0.164$ as a function of asymptotic size for five values of m_1 . When $m_1 = 0$, asymptotic size does not affect predicted age at maturity (as in the standard Beverton GML)

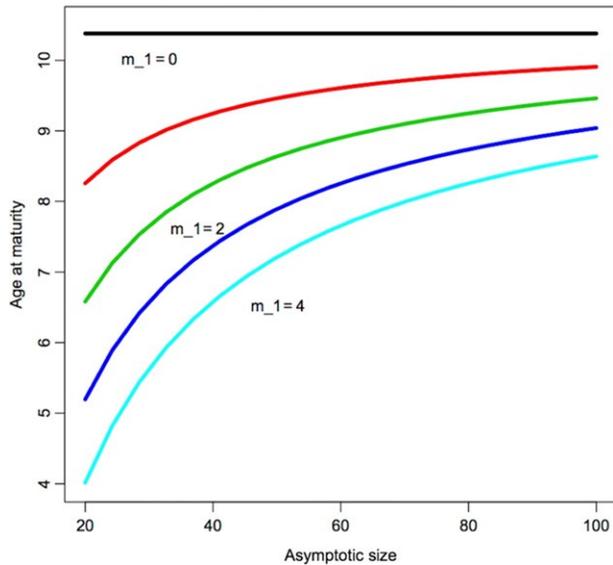


FIGURE 4 Predicted age at maturity as a function of asymptotic size for five values of m_1 . The second curve from the top has $m_1 = 3$, and the fourth curve from the top has $m_1 = 1$. When $m_1 = 0$ we are back to Beverton's basic result so that asymptotic size does not influence age at maturity. [Colour figure can be viewed at wileyonlinelibrary.com]

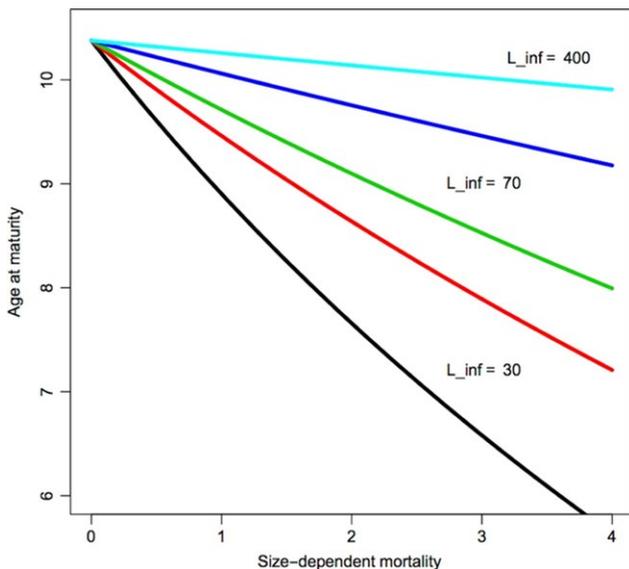


FIGURE 5 Predicted age at maturity as a function of the rate size-dependent natural mortality for five values of L_∞ . The second curve from the top has $L_\infty = 150$, and the fourth curve from the top has $L_\infty = 400$. When L_∞ is very large (more specifically in the limit of unbounded asymptotic size) age at maturity does not depend upon on the rate of size-dependent mortality. [Colour figure can be viewed at wileyonlinelibrary.com]

but otherwise it does and clearly interacts with the size-dependent mortality. In Figure 5, I plot age at maturity as a function of m_1 for five values of asymptotic size; this is another way of representing the results—and shows that even when L_∞ is very large there is still an effect on the predicted age at maturity. These curves all intersect at $m_1 = 0$ because in that case the predicted age at maturity does not depend on asymptotic size.

An important practical implication (and testable prediction) of these results is that we predict age of maturity to be higher in populations of the same species having larger asymptotic sizes.

5 | DISCUSSION

5.1 | The inverse life-history problem

Solving Equation (5) for an estimate of the rate of natural mortality, as in Equation (6)—the inverse life-history problem—opens an avenue for computing the distribution of the rate of natural mortality as every mature fish provides information to us on growth rate, age at maturity (from scales or otoliths) and the size fecundity exponent. By employing this approach, and modern statistical methods as in Dick et al. (2017), we will now have plenty of data for estimating a constant value of M , rather than the usual shortage of data for estimating natural mortality. In the examples that I showed here, I did not have full distributions for growth rate or age at maturity, but there is no reason that the approach Dick et al. (2017) used could not be applied to data on growth rate and age at maturity.

To be sure, Equation (6) has its limitations, which is why the results presented here should be considered illustrative rather than formal results of research. First, as mentioned above, the distributions that I used for k and a_{50} were ad hoc. Second, Equation (6) applies only to a semelparous fish or an iteroparous fish with no growth after maturity and with size-independent M . However, when applying it, one can easily check how close the ratio $L_m/L_\infty = 1 - e^{-ka_M}$ is to 1; the greater this ratio, the better the assumption of no growth after maturity. For example, for the tunas in Figure 1, the fraction $L(a_{mat})/L_\infty$ is 0.65, 0.63 and 0.82 for skipjack tuna, yellowfin tuna and southern bluefin tuna, respectively. Whether the much closer fit of southern bluefin tuna to Hampton's (1991) result is due to the assumption of no growth after maturity being more closely met or to chance remains an open and interesting question.

If we were to apply the same simulation approach to Equation (18), the result would be a distribution for the combination of m_0 and m_1 shown on the right-hand side of the equation. Thus, we would not be able to uniquely identify these parameters, but only the combination, similar to the results shown in Figure 3.

I have not been able to find relatively simple analogues of Equation (18) for the iteroparous fish with no growth after maturity. If one a priori chooses age at maturity (Charnov et al., 2013) then progress can be made, but otherwise numerical solutions are needed to determine optimal age at maturity.

The case of the iteroparous fish with substantial growth after maturity—which encompasses many species across many genera—requires

a completely different approach as we now need a life-history model in which resources are allocated between growth and maturity. The natural framework for this is state-dependent life-history theory implemented by stochastic dynamic programming (e.g. Mangel, 2015 and references there-in). The life-history model will produce predictions of behaviour, allocation and reproduction conditioned on the environment and the inverse problem is to take those observations and make inferences about the environment (e.g. abundance of food, rate of mortality) that generated them.

Most importantly, the inverse method provides an intraspecific approach to estimating distributions of mortality that will complement existing interspecific approaches based on statistical methods.

5.2 | Size-dependent mortality

This work resolves some questions and raises others.

First, Gislason et al. (2010, pp. 5–6) wrote regarding Equation (2) in their paper (Equation (1)) “The significant positive relationship between M and L_∞ is somewhat surprising, but may be caused by a trade-off between growth and mortality”. Their result is indeed surprising as we expect that in the limnological and marine environments gape is a major determinant of the rate of mortality and thus large individuals are more likely to survive than smaller individuals. Gislason et al. (2010) offer a variety of scaling arguments to show that natural mortality varies inversely with a power of asymptotic size.

The answer may be much simpler, however, when we recognize that L in Equation (1) is $L_\infty(1 - e^{-k(a-a_0)})$. Thus, Equation (1) can also be written with mortality as a function of age a as

$$M_g(a) = M_g(L(a)) = e^{0.55} \cdot k \cdot L_\infty^{1.44} / [L_\infty(1 - e^{-k(a-a_0)})]^{1.61} \\ = e^{0.55} \cdot \frac{k}{[1 - e^{-k(a-a_0)}]^{1.61}} \cdot L_\infty^{-0.17} \quad (19)$$

which is exactly the same scaling with respect to asymptotic size that Gislason et al. (2010) reach (their Equation (3)) with a much longer argument requiring assumptions about the size-independent measurements of natural mortality.

Second, writing $M_c(L(a))$ as a function of age

$$M_c(a) = M_c(L(a)) = k \cdot \left(\frac{L_\infty}{L_\infty(1 - e^{-k(a-a_0)})} \right)^{1.5} = \frac{k}{(1 - e^{-k(a-a_0)})^{1.5}} \quad (20)$$

shows that the rate of natural mortality is proportional to k with an age-dependent proportionality constant that also depends upon k but is independent of asymptotic size. Charnov et al. (2013) noted that Equation (2) is as good a statistical fit to the data as Equation (1); that is Equations (19) and (20) appear to be statistically the same; why this is so remains an open question.

These equations remind us not to forget that asymptotic size is not a fundamental quantity in von Bertalanffy growth, but a derived one involving growth rate k and anabolic factors such as the density and quality of food in the environment (Mangel, 2006 pp. 25–26, appendix in Charnov et al., 2013). If the latter are summarized by anabolic parameter q , then $L_\infty = q/k$. Snover, Watters, and Mangel (2005) use

this recognition in their study of the growth of coho salmon as it transitions from fresh to seawater.

Third, an open question is why Beverton’s original analysis works as well as it does when applied to fish (or other organisms—see Beverton, 1992) with substantial growth after maturity and size-dependent mortality.

Fourth, the form of size-dependent natural mortality that I propose (Equation (9)), requires two parameters. As I have shown above, by treating the regression analysis of Gislason et al. (2010) as the true state of nature, we can fit the mortality function in Equation (9) quite accurately. Clearly, if one had tagging data, then each fish would provide information for obtaining the parameters m_0 and m_1 . In addition, Carlson et al. (2010) showed that one can develop Bayesian methods for determining m_0 and m_1 in which one only has size distributions at one time and a subsequent time.

Fifth, notion of dimensionless ratios (Mangel 2005) becomes more complicated when we recognize that mortality is size dependent. Both k and M are rates, so that their ratio (either k/M or M/k) is dimensionless and this played an important role in Beverton’s original GML theory and in Charnov’s development of life-history invariants (e.g. Charnov, 1993). Even the simplest form of size/age-dependent mortality (Equation (20)) does not give a ratio that is constant, but one that depends upon age.

Hence, it may be appropriate to focus not on mortality but on survival to maximum age. Regardless of the form of size-dependent mortality, survival to maximum age is

$$S(a_{\max}) = \exp \left[- \int_0^{a_{\max}} M(L(a)) da \right] \quad (21)$$

and it may be valuable in future studies to define an effective rate of mortality \hat{M} by setting $S(a_{\max}) = \exp(-\hat{M}a_{\max})$. Such an effective rate of natural mortality was used by Andrews and Mangel (2012) in a study of long-lived fish and data poor-stock assessments. If there is no obvious choice for a_{\max} , one might choose either the age of the oldest individual of a species that has been observed plus some additional number of years or the age at which survival reaches a fixed small number (e.g. the 1 in 10 million fish, Mangel (2003)). With this effective rate of mortality, we can once again explore dimensionless ratios.

This logic is implicit in estimates for a constant rate of mortality that rely on maximum age (e.g. reviews in Hoenig 1983; Hoenig et al., 2016; Kenchington, 2014; Then, Hoenig, Hall, & Hewitt, 2015). That is, if \hat{a}_{\max} is the maximum observed age

$$e^{-\hat{M}a_{\max}} = \exp \left[- \int_0^{\hat{a}_{\max}} M(L(a)) da \right] \quad (22)$$

so that the effective rate of mortality

$$\hat{M} = \frac{\int_0^{\hat{a}_{\max}} M(L(a)) da}{\hat{a}_{\max}} \quad (23)$$

which gives us an interpretation for the proportionality coefficient in maximum age-based methods for estimating the rate of (constant) mortality.

Sixth, it is clear that rules of thumb for setting fishing mortality as a proportion of natural mortality also becomes much more complicated when the rate of natural mortality is not constant. If length is a deterministic function of age, then length-dependent mortality and age-dependent mortality are interchangeable and rules of thumb can be developed (e.g. Kindsvater, Mangel, Reynolds, & Dulvy, 2016; Kindsvater, Reynolds, Sadovy de Mitcheson, & Mangel, 2017). Andrews and Mangel (2012) and Mangel et al. (2013) show how we can decide when putatively size-dependent length-dependent mortality can be treated as nearly constant in a stock assessment.

6 | CONCLUSION

Nearly 60 years on, the ideas developed by Sidney Holt and expanded by Ray Beverton into a theory of GML continue to provide stimulus for exploration. The inverse life-history problem is a direct descendant of Beverton's theory of GML and extending the theory of GML for size-dependent mortality will provide opportunities for both new analysis and new empirical studies.

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APPENDIX: The Semelparous Fish with $M_g(L)$ and $M_c(L)$

From Equations (14–16) it is clear that the general condition for optimal age at maturity will be

$$M(L(a))L(a) = bL_\infty ke^{-ka}$$

Using $M_g(L)$ from Equation (1) we have

$$\left(e^{0.55} \cdot k \cdot L_\infty^{1.44} / L^{1.61} \right) L(a) = bL_\infty ke^{-ka}$$

which can be simplified to give

$$\frac{e^{0.55}}{bL_\infty^{0.27}} = e^{-ka}(1 - e^{-ka})^{0.61}$$

This is a transcendental equation for e^{-ka} , requiring a numerical method for finding its solution. Even when a solution can be found, it will be difficult to interpret.

Using $M_c(L)$ we begin with

$$k \left[\frac{L_\infty}{L(a)} \right]^{1.5} L(a) = bL_\infty ke^{-ka}$$

which can be simplified to

$$L_\infty = b^2 e^{-2ka} L_\infty (1 - e^{-ka})$$

leading to a cubic equation for $x = e^{-ka}$

$$x^2(1-x)b^2 = 1$$

which does not have a tractable analytical solution but clearly shows that asymptotic size will in fact not affect age at maturity.