



## MODEL FOR THE INSTANTANEOUS RATE OF TOTAL MORTALITY $F(a, t) + M(a, t)$

The instantaneous rate of natural mortality of an animal population is a population characteristic, whereas its surrogates are usually characteristics of the individuals in the population. To establish a relationship, for a suite of species, between the instantaneous rate of natural mortality of a population and surrogates of its individuals, one needs to set up a population dynamics model for each species, identify its parameters common to all species concerned, and estimate these parameters from existing data on that suite of species. For easy exposition, however, I will omit the species index, unless otherwise stated.

Now, let  $N(a, t) \geq 0$ ,  $0 \leq a'_0 \leq a < \infty$ ,  $-\infty \leq t_0 \leq t < \infty$ , denote the number of animals of age  $a$  at time  $t$  in a natural population, with an average age at birth  $a'_0$  and reference time  $t_0$ . The change in  $N(a, t)$  in a time interval of length  $\Delta t$  is assumed to be proportional to  $N(a, t)$ , such that

$$\lim_{\Delta t \rightarrow 0} \frac{N(a + \Delta a, t + \Delta t) - N(a, t)}{\Delta t} = -[F(a, t) + M(a, t)]N(a, t),$$

where  $F(a, t) \geq 0$  and  $M(a, t) \geq 0$  are, respectively, the instantaneous rate of fishing and natural mortalities of animals of age  $a$  at time  $t$ . The instantaneous rate of fishing mortality  $F(a, t)$  is included here to cater for human exploited populations;  $F(a, t) = 0$  for unexploited populations. Finally, notice that although  $\Delta a = \Delta t$  or  $\frac{da}{dt} = 1$  for many fisheries applications,  $\Delta a \neq \Delta t$  or  $\frac{da}{dt} \neq 1$ , as when fish age  $a$  is measured in years and time  $t$  in months. Expansion of  $N(a + \Delta a, t + \Delta t)$  in the neighbourhood of  $(a, t)$  as  $N(a + \Delta a, t + \Delta t) = N(a, t) + \frac{\partial N(a, t)}{\partial a} \Delta a + \frac{\partial N(a, t)}{\partial t} \Delta t + O(\Delta t^2)$  and passing to the limit  $\Delta t \rightarrow 0$  give

$$\lim_{\Delta t \rightarrow 0} \frac{N(a + \Delta a, t + \Delta t) - N(a, t)}{\Delta t} = \frac{\partial N(a, t)}{\partial a} \frac{da}{dt} + \frac{\partial N(a, t)}{\partial t},$$

which leads to

$$\frac{\partial N(a, t)}{\partial a} \frac{da}{dt} + \frac{\partial N(a, t)}{\partial t} = -[F(a, t) + M(a, t)]N(a, t), \quad (1)$$

from which

$$F(a, t) + M(a, t) = -\frac{1}{N(a, t)} \left[ \frac{\partial N(a, t)}{\partial a} \frac{da}{dt} + \frac{\partial N(a, t)}{\partial t} \right]. \quad (2)$$

It can be proved (see the Appendix) that, at temporal equilibrium, under the assumption of the most stable age distribution, and if  $\frac{da}{dt} = 1$ , equation (2) becomes

$$F(a, t) + M(a, t) = -\frac{1}{N(a, t)} \frac{\partial N(a, t)}{\partial a} \frac{da}{dt} = \frac{1}{\lambda} \approx \frac{1}{\mu}, \quad (3)$$

where  $\lambda = \lambda(t)$ , redefined from  $\lambda_1(t)$  in the Appendix, and  $\mu = \mu(t)$  are, respectively, the characteristic age and mean age of the equilibrial and most stable population. These assumptions are not as restrictive as they seem. For practical purposes and of necessity, they are made implicitly in almost all measurements of  $M(a, t)$ , many other types of data, and many biological models.

Now, both characteristic age  $\lambda$  and mean age  $\mu$  can be expressed in easily measurable quantities of an animal individual, including its age, length, and mass. To do so, let an arbitrary measurable quantity  $S(a)$  be given, as a function of age  $a$ , by

$$S(a) = g(a), \quad \text{or} \quad (4)$$

$$a = g^{-1}(S(a)), \quad (5)$$

where  $g^{-1}(S(a))$  is the inverse function (assumed to exist) of  $g(a)$ . Substitution of equation (5) for  $a = \lambda$  into equation (3) yields the general model for calculating the value of  $F(a, t) + M(a, t)$  from values of its surrogates

$$F(a, t) + M(a, t) = \frac{1}{g^{-1}(S(\lambda))} \approx \frac{1}{g^{-1}(S(\mu))}, \tag{6}$$

from which age-, length-, and mass-based models result.

### AGE-BASED MODELS

Little information is available on how an age-based quantity  $T$  (e.g., age at maturity, longevity, and observed maximum age) of a population of animals varies with the characteristic age  $\lambda$  or mean age  $\mu$  of its equilibril population. However,  $T = S(\lambda)$  can be approximated by its Taylor series expansion of the first order in the neighbourhood of  $\lambda_0$ , i.e.,

$$S(\lambda) = T = S(\lambda_0) + \frac{dS(\lambda_0)}{d\lambda} (\lambda - \lambda_0) + O((\lambda - \lambda_0)^2). \tag{7}$$

Substitution of equation (7) into equation (3) yields

$$F(a, t) + M(a, t) = \frac{\alpha}{T + \beta}, \tag{8}$$

where  $\alpha = \frac{dS(\lambda_0)}{d\lambda}$  and  $\beta = \lambda_0 \frac{dS(\lambda_0)}{d\lambda} - S(\lambda_0) - O((\lambda - \lambda_0)^2)$  are parameters (across all species in a group) to be estimated. Similarly, a second-order Taylor series expansion of  $T = S(\lambda)$  in the neighbourhood of  $\lambda_0$  yields

$$S(\lambda) = T = S(\lambda_0) + \frac{dS(\lambda_0)}{d\lambda} (\lambda - \lambda_0) + \frac{d^2S(\lambda_0)}{d\lambda^2} (\lambda - \lambda_0)^2 + O((\lambda - \lambda_0)^3).$$

Substitution of this equation into equation (3) gives

$$F(a, t) + M(a, t) = \frac{\alpha}{\varepsilon + \sqrt{\beta + 2\alpha T}},$$

where

$$\begin{aligned} \alpha &= \frac{d^2S(\lambda_0)}{d\lambda^2}, \\ \beta &= \left(\frac{dS(\lambda_0)}{d\lambda}\right)^2 - 2\left[S(\lambda_0) + O(\lambda - \lambda_0)^3\right] \frac{d^2S(\lambda_0)}{d\lambda^2}, \quad \text{and} \\ \varepsilon &= \lambda_0 \frac{d^2S(\lambda_0)}{d\lambda^2} - \frac{dS(\lambda_0)}{d\lambda} \end{aligned}$$

are parameters (across all species in a group) to be estimated. In using an age-based model, it is important to choose an age-based quantity, such that  $\alpha$ ,  $\beta$ , and  $\varepsilon$  are constant across all species of interest.

Notice that equation (8) differs from, but can be reduced to, Ohsumi's [1, p. 401, lines 10-19] ( $T = T$ ,  $F(a, t) = 0$ ,  $M(a, t) = M$ ,  $\alpha = \log(a)$ , and  $\beta = 0$ ), to Hoenig's equation (2) ( $\alpha = -\log(k)$ ,  $\beta = 0$ ,  $Z = F(a, t) + M(a, t)$ , and  $T = t_L$ ) [4], and to Jensen's equation (7) ( $F(a, t) = 0$ ,  $\alpha = 1.65$ ,  $\beta = 0$ , and  $T = x_m$ ) [6]. Their equations were, however, derived under questionable assumptions. Ohsumi [1] defined the longevity of a population as the age to which only one individual is observed to survive. This definition gives an underestimate of longevity, for that individual may well live for some time after observation. Similarly, Hoenig defined it as the age to which an arbitrarily small proportion of a stock survive [4]. Finally, Jensen's equation (5), and its resulting equations, assume that fish of a stock mature when their fecundity function  $f(a)$  at age  $a$  takes its maximum value [6]. Alternatively, one can maximize their reproductive output in their life history  $\int_{a_m}^{\infty} f(a) da$  to yield an average age at maturity  $a_m = a_0'$ ! Thus, animals should mature as early as possible and, in fact, at birth, to maximize their reproductive output in their lives. Although some species of insects adopt this rather interesting life history strategy, the great majority of species of animals do not.

## LENGTH-BASED MODELS

In this section, I will relate characteristic age  $\lambda$  and mean age  $\mu$  of an equilibrated population to a length-based quantity. Thus, consider the length of its individuals at age  $a$   $L(a)$ . Specifically, I will now consider the most commonly used von Bertalanffy, logistic, and Gompertz growth equations, which, in a differential equation, are given, respectively, by

$$\begin{aligned} \frac{dL(a)}{da} &= K(L_\infty - L), & 0 \leq K, \quad 0 \leq L \leq L_\infty, \quad 0 \leq \frac{dL(a)}{da} \leq KL_\infty, \\ \frac{dL(a)}{da} &= KL \left(1 - \frac{L}{L_\infty}\right), & 0 \leq K, \quad 0 \leq L \leq L_\infty, \quad 0 \leq \frac{dL(a)}{da} \leq \frac{1}{4}KL_\infty, \quad \text{and} \\ \frac{dL(a)}{da} &= KL \log_e \left(\frac{L_\infty}{L}\right), & 0 \leq K, \quad 0 \leq L \leq L_\infty, \quad 0 \leq \frac{dL(a)}{da} \leq \frac{1}{e}KL_\infty, \end{aligned}$$

with von Bertalanffy, logistic or Gompertz parameters  $(K, L_\infty)$ . Note that  $K$  and  $L_\infty$  have exactly the same meaning in those equations:  $K$  is the growth rate of an individual animal;  $L_\infty$  is its asymptotic size. Solution of these equations, each as an initial value problem with  $L(a)|_{a=a_0} = L(a_0)$ , yields, respectively [8],

$$\begin{aligned} L(a) &= L_\infty - [L_\infty - L(a_0)]e^{-K(a-a_0)}, \\ L(a) &= \frac{L(a_0)L_\infty}{L(a_0) + [L_\infty - L(a_0)]e^{-K(a-a_0)}}, \quad \text{and} \\ L(a) &= L_\infty \left[\frac{L(a_0)}{L_\infty}\right]^{e^{-K(a-a_0)}}. \end{aligned}$$

It should be stressed here that  $L(a_0)$  is defined as the length of an individual at age  $a_0$ :  $a_0$  can be any age of that individual right from its genesis to its death, and  $L(a_0)$  its corresponding length. These equations can be rewritten as

$$a = a_0 - \frac{1}{K} \log \left( \frac{L_\infty - L(a)}{L_\infty - L(a_0)} \right), \quad (9.1)$$

$$a = a_0 - \frac{1}{K} \log \left( \frac{L(a_0)[L_\infty - L(a)]}{L(a)[L_\infty - L(a_0)]} \right), \quad \text{and} \quad (9.2)$$

$$a = a_0 - \frac{1}{K} \log \left( \frac{\log(L_\infty/L(a))}{\log(L_\infty/L(a_0))} \right). \quad (9.3)$$

Substitution of equations (9.1)–(9.3) for  $a = \lambda$  into equation (3) yields, respectively,

$$F(a, t) + M(a, t) = \frac{K}{Ka_0 - \log((L_\infty - L(\lambda)) / (L_\infty - L(a_0)))}, \quad (10.1)$$

$$F(a, t) + M(a, t) = \frac{K}{Ka_0 - \log(L(a_0)[L_\infty - L(\lambda)] / (L(\lambda)[L_\infty - L(a_0)])}, \quad (10.2)$$

$$F(a, t) + M(a, t) = \frac{K}{Ka_0 - \log(\log(L_\infty/L(\lambda)) / \log(L_\infty/L(a_0)))}. \quad (10.3)$$

All growth parameters and variables are now in equations (10.1)–(10.3). But, what is to be estimated from the (multispecific) data? A parameter must be invariant, at least approximately, across all species of interest. Both  $L(\lambda)$  and  $a_0$  vary across all species, and hence, are not appropriate parameters. However, the logarithms of the relative quantities and  $Ka_0$  in these equations vary much less in extent across all species, or a group of species. They are therefore assumed, to the first approximation, to be a composite parameter across all species, in which case equations (10.1)–(10.3) all become

$$F(a, t) + M(a, t) = \frac{K}{\gamma}, \quad (11)$$

but with parameter

$$\begin{aligned} \gamma &= Ka_0 - \log \left( \frac{L_\infty - L(\lambda)}{L_\infty - L(a_0)} \right), \\ \gamma &= Ka_0 - \log \left( \frac{L(a_0) [L_\infty - L(\lambda)]}{L(\lambda) [L_\infty - L(a_0)]} \right), \quad \text{and} \\ \gamma &= Ka_0 - \log \left( \frac{\log(L_\infty/L(\lambda))}{\log(L_\infty/L(a_0))} \right). \end{aligned}$$

In using one of the length-based models, one needs to choose a length-based quantity  $L(a)$ , a reference length  $L(a_0)$ , and a reference age  $a_0$ , such that  $\gamma$  is constant across all species concerned. Clearly, equation (11) has the same functional form as Jensen's equation (8) [6], which was, however, derived under a restrictive assumption (see above).

### MASS-BASED MODELS THROUGH LENGTH

To relate characteristic age  $\lambda$  and mean age  $\mu$  of an equilibrated animal population to a mass-based quantity through a length-based quantity, one only needs to replace  $L(\lambda)$  in equation (11) with its associated mass-based quantity. For example, let the general allometric equation

$$S(a) = c' + a'L(a)^{b'}, \quad (\text{see [9]}) \quad \text{or} \quad (12)$$

$$L(a) = \left( \frac{S(a) - c'}{a'} \right)^{-b'} \quad (13)$$

represent the relationship between the mass of an animal  $S(a)$  and its length  $L(a)$  at age  $a$ , with allometric parameters  $a' > 0$ ,  $b' > 0$ , and  $c' \leq 0$ . Substitution of equation (13) for  $a = \lambda$  into equation (11) yields

$$F(a, t) + M(a, t) = \frac{K}{\delta}, \quad (14)$$

with parameter

$$\begin{aligned} \delta &= Ka_0 - \log \left( \frac{L_\infty - ((S(\lambda) - c')/a')^{-b'}}{L_\infty - L(a_0)} \right), \\ \delta &= Ka_0 - \log \left( \frac{L(a_0) [L_\infty - ((S(\lambda) - c')/a')^{-b'}]}{L(\lambda) [L_\infty - L(a_0)]} \right), \quad \text{and} \\ \delta &= Ka_0 - \log \left( \frac{\log(L_\infty ((S(\lambda) - c')/a')^{b'})}{\log(L_\infty/L(a_0))} \right). \end{aligned}$$

Similarly, models alternative to Gunderson's [2] and Gunderson and Dygert's [5] models can be readily derived for predicting the instantaneous rate of natural mortality of animals from their gonadosomatic index, because their gonadosomatic index is a function of their length.

### DATA AND ANALYSIS

Use of equation (8) to estimate  $\alpha$  and  $\beta$  (assumed to be constant over all species in a group) requires data on the instantaneous rate of fishing mortality  $F(a, t)$ , the instantaneous rate of natural mortality  $M(a, t)$  and an age-based quantity  $T$  for some species in a group; use of equation (11) to estimate  $\gamma$  (assumed to be constant over all species in a group) requires data on  $F(a, t)$ ,  $M(a, t)$  and growth rate  $K$  for some species in a group. However, for many species, the

estimates of  $F(a, t)$  are usually not very reliable;  $M(a, t)$  is usually substantially overestimated. The problem with  $F(a, t)$  can be eliminated or reduced by using data from unexploited or lightly exploited populations. Unfortunately, almost all estimates of  $M(a, t)$  come from heavily fished populations.

To illustrate my method, three sets of data from three groups of animals are analysed. Since reliable estimates of  $F(a, t)$  are not readily available, in this analysis, they are either assumed to be zero or estimated as a parameter common to all species concerned. Thus, fitting of equation (8) to Ohsumi's data [1] on the instantaneous rate of natural mortality  $M(a, t)$  of cetaceans as a function of their observed maximum age  $T$ , under the assumption that the errors in  $M(a, t)$  are independent normal variates, yields  $\hat{F}(a, t) = 0.0042(\pm 0.0197) \cdot \text{yr}^{-1}$ ,  $\hat{\alpha} = 4.8801(\pm 2.1502)$ ,  $\hat{\beta} = -1.1525(\pm 10.5027) \text{yr}$ ,  $F_{3,16} = 383.8488$ ,  $P < 0.0001$ ,  $r^2 = 0.9863$ ,  $n = 19$  (Figure 1). Because of the relatively high estimates of the standard errors of  $\hat{F}(a, t)$  and  $\hat{\beta}$ , three submodels of equations (8) were also fitted. For equation (8) ( $F(a, t) = 0$ ),  $\hat{\alpha} = 4.4418(\pm 0.3486)$ ,  $\hat{\beta} = -3.2320(\pm 3.1042) \text{yr}$ ,  $F_{2,17} = 609.7054$ ,  $P < 0.0001$ ,  $r^2 = 0.9863$ ,  $n = 19$ ; for equation (8) ( $\beta = 0$ ),  $\hat{F}(a, t) = 0.0062(\pm 0.0063) \cdot \text{yr}^{-1}$ ,  $\hat{\alpha} = 5.1144(\pm 0.3693)$ ,  $F_{2,17} = 611.2678$ ,  $P < 0.0001$ ,  $r^2 = 0.9863$ ,  $n = 19$  (Figure 1). The relatively high estimates of the standard errors of  $\hat{\beta}$  and  $\hat{F}(a, t)$  and little change in the coefficient of determination  $r^2$  from fitting both submodels indicate that, for this set of data,  $F(a, t)$  and  $\beta$  can be set to zero. So, fitting of equation (8) to the same data on the instantaneous rate of natural mortality  $M(a, t)$  of cetaceans as a function of their observed maximum age  $T$ , under the assumptions that  $F(a, t) = 0$ ,  $\beta = 0$ , and the errors in  $M(a, t)$  are independent normal variates, yields  $\hat{\alpha} = 4.7725(\pm 0.1365)$ ,  $F_{1,18} = 1222.0446$ ,  $P < 0.0001$ ,  $r^2 = 0.9855$ ,  $n = 19$  (Figure 1). Notice that, in all analyses, the observed maximum age of a cetacean population is about five times as high as the mean age of all individuals in the population, as is consistent with a well-known fact that the maximum age of any population

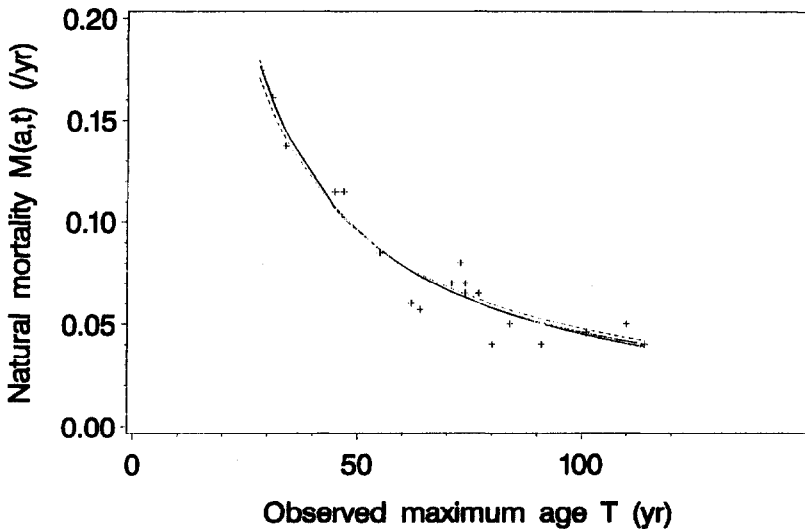


Figure 1. Observed (●) and expected ( $\beta = 0$ , ---; all other cases, —) instantaneous rate of natural mortality as a function of observed maximum age for cetaceans, as given by equation (8) ( $\alpha \neq 0$ ) and its submodels.

is at least as great as and generally much greater than the mean age of all individuals in the population.

Indeed, equation (8) (with a residual sum of squares of 0.0017268 and residual degrees of freedom of 16) is not significantly different from its submodel equation (8) ( $F(a, t) = 0$ ) (with a residual sum of squares of 0.0017325 and residual degrees of freedom of 17) ( $F_{1,16} = 0.0532$ ,  $P = 0.8206$ ) or equation (8) ( $\beta = 0$ ) (with a residual sum of squares of 0.0017281 and residual

degrees of freedom of 17) ( $F_{1,16} = 0.0127, P = 0.9117$ ) [10]. Similarly, neither equation (8) ( $F(a, t) = 0$ ) nor equation (8) ( $\beta = 0$ ) is significantly different from its submodel equation (8) ( $F(a, t) = 0$  and  $\beta = 0$ ) (with a residual sum of squares of 0.0018290 and residual degrees of freedom of 18) ( $F_{1,17} = 0.9473, P = 0.3441; F_{1,17} = 0.9926, P = 0.3331$ ). The final and most parsimonious model is, therefore, equation (8) ( $F(a, t) = 0$  and  $\beta = 0$ ).

Fitting of equation (11) to Gunderson and Dygert's data [5] on the instantaneous rate of natural mortality  $M(a, t)$  of fishes as a function of their fishing mortality  $F(a, t)$  and growth rate  $K$ , under the assumption that the errors in  $M(a, t)$  are independent normal variates, yields  $\hat{F}(a, t) = -0.0652(\pm 0.1246) \cdot \text{yr}^{-1}, \hat{1}/\gamma = 1.0632(\pm 0.4453), F_{1,18} = 5.700, P = 0.0281, r^2 = 0.2405, n = 20$  (Figure 2). Again, the relatively high estimate of the standard error of  $\hat{F}(a, t)$  indicates that, for this set of data,  $F(a, t)$  can be set to zero. Again, fitting of equation (11) to these data on the instantaneous rate of natural mortality  $M(a, t)$  of fishes as a function of growth rate  $K$ , under the assumptions that  $F(a, t) = 0$  and the errors in  $M(a, t)$  are independent normal variates, yields  $\hat{1}/\gamma = 1.2718(\pm 0.1944), F_{1,19} = 42.8242, P = 0.0001, r^2 = 0.6927, n = 20$  (Figure 2).

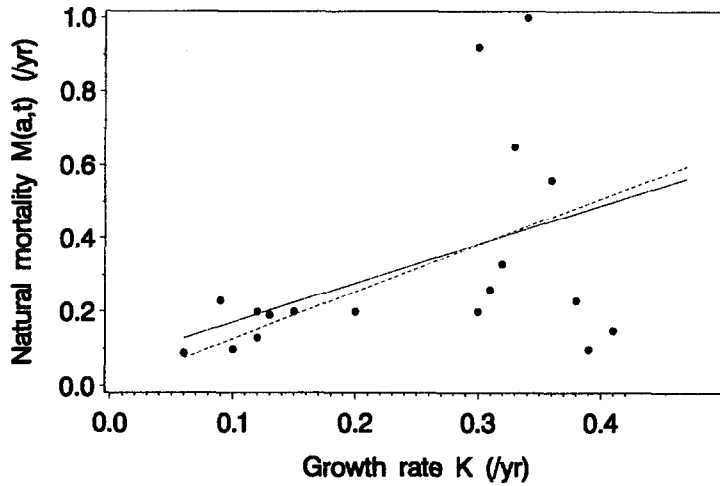


Figure 2. Observed (•) and expected ( $F(a, t) \neq 0, —; F(a, t) = 0, - - -$ ) instantaneous rate of natural mortality as a function of growth rates of fishes, as given by equation (11).

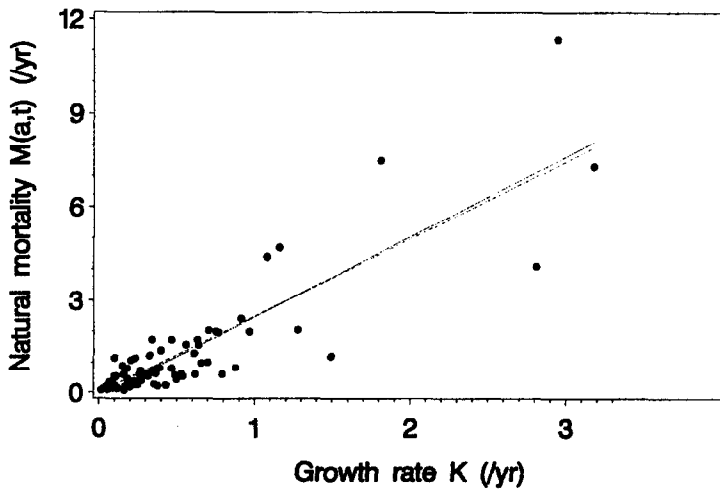


Figure 3. Observed (•) and expected ( $F(a, t) \neq 0, —; F(a, t) = 0, - - -$ ) instantaneous rate of natural mortality as a function of growth rates of benthic invertebrates, as given by equation (11).

Fitting of equation (11) to Brey and Gage's data [7] on the instantaneous rate of natural mortality  $M(a, t)$  of benthic invertebrates as a function of their fishing mortality  $F(a, t)$  and growth rate  $K$ , under the assumption that the errors in  $M(a, t)$  are independent normal variates, yields  $\hat{F}(a, t) = 0.1077(\pm 0.1251) \cdot \text{yr}^{-1}$ ,  $\hat{1}/\gamma = 2.5709(\pm 0.1629)$ ,  $F_{1,80} = 249.2049$ ,  $P = 0.0001$ ,  $r^2 = 0.7570$ ,  $n = 82$  (Figure 3). Similarly, fitting of equation (11) to these data on the instantaneous rate of natural mortality  $M(a, t)$  of benthic invertebrates as a function of growth rate  $K$ , under the assumptions that  $F(a, t) = 0$  and the errors in  $M(a, t)$  are independent normal variates, yields  $\hat{1}/\gamma = 2.4825(\pm 0.1262)$ ,  $F_{1,81} = 386.6960$ ,  $P = 0.0001$ ,  $r^2 = 0.8268$ ,  $n = 82$  (Figure 3).

## DISCUSSION

This work demonstrates that the instantaneous rate of natural mortality of animals in a natural population can be derived as a function of one or more of its surrogates, thereby providing age-, length-, and mass-based models, or models based on other biologically meaningful quantities for its estimation. Although intended mainly for fishery applications, these models also apply to a greater variety of animals.

The instantaneous rate of natural mortality of an animal population is one of the most difficult and elusive quantities to estimate. In fact, its estimates are often substantially positively biased. Like previous models, those developed above require that uncertainties in  $F(a, t) + M(a, t)$  be negligible to avoid their propagation to estimates of parameters.

The above models assume that the populations concerned are at temporal equilibrium. Such an assumption is necessary but is not, however, as restrictive as it seems. In fact, it underlies most biological studies. Although unlikely to be valid over long time scales, it should be so over reasonably short time scales. Thus, these models can be used to study long-term changes in the instantaneous rate of natural mortality of animals' populations by computing short-term ones.

Finally, some age-based models may be better than length- or mass-based ones, because certain age-based quantities are more reliably measured. Also, the growth rates of length- or mass-based quantities may have different interpretations and hence can be as elusive as  $M(a, t)$  itself. That is probably why equation (11) was not fitted to Gunderson and Dygert's data [5] and Brey and Gage's data [7] very well.

## APPENDIX

### DERIVATION OF EQUATION (3)

At temporal equilibrium, i.e.,  $\frac{\partial N(a, t)}{\partial t} = 0$ , equation (2) becomes

$$F(a, t) + M(a, t) = -\frac{1}{N(a, t)} \frac{\partial N(a, t)}{\partial a} \frac{da}{dt}. \quad (\text{A1})$$

There are an infinite number of ways for allocating a total of  $N(t)$  individuals at time  $t$  of a population at temporal equilibrium over the (continuous) age interval  $[\alpha, \beta]$ . How can then  $N(a, t)$  be determined uniquely as a function of age  $a$ ? The most probable distribution of this infinitum must be the most stable in the absence of large environmental disturbances. This assumption is valid for many species of large sizes, at least approximately and in the short-term. Under this assumption,  $N(a, t)$  as a function of age  $a$  at time  $t$  can be found, as a simple variation problem, by maximizing the entropy of the distribution function

$$-\int_{\alpha}^{\beta} p(a, t) \log(p(a, t)) da \quad (\text{A2})$$

under the constraints that

$$1 = \int_{\alpha}^{\beta} p(a, t) da \quad \text{and} \quad \mu(t) = \int_{\alpha}^{\beta} ap(a, t) da,$$



where  $p(a, t) = N(a, t)/N(t)$ . These constraints are, of course, justified mathematically [11]. To solve this variation problem, let

$$H = -p(a, t) \log(p(a, t)) + \lambda_0(t)p(a, t) - \frac{1}{\lambda_1(t)}ap(a, t),$$

where  $\lambda_i(t)$ s are the Lagrange multipliers to be determined from the constraints. Now, differentiating  $H$  with respect to  $p(a, t)$  and letting

$$\frac{dH}{dp(a, t)} = -[\log(p(a, t)) + 1] + \lambda_0(t) - \frac{a}{\lambda_1(t)} = 0$$

yield

$$p(a, t) = e^{\lambda_0(t)-1-a/\lambda_1(t)}. \tag{A3}$$

Equation (A3) does correspond to the maximum entropy or maximum value of equation (A2) of  $\mu(t)/\lambda_1(t) + 1 - \lambda_0(t)$ , for  $\frac{d^2H}{dp(a, t)^2} = -1/p(a, t) < 0$ . Substitution of equation (A3) into the constraint  $1 = \int_{\alpha}^{\beta} p(a, t) da$  gives

$$1 = \int_{\alpha}^{\beta} p(a, t) da = \int_{\alpha}^{\beta} e^{\lambda_0(t)-1-a/(\lambda_1(t))} da = \lambda_1(t)e^{\lambda_0(t)-1}e^{-\alpha/\lambda_1(t)} \left[ 1 - e^{-(\beta-\alpha)/\lambda_1(t)} \right],$$

from which

$$p(a, t) = \frac{1}{\lambda_1(t) \left[ 1 - e^{-(\beta-\alpha)/\lambda_1(t)} \right]} e^{-(a-\alpha)/\lambda_1(t)}. \tag{A4}$$

Applying the constraint  $\mu(t) = \int_{\alpha}^{\beta} ap(a, t) da$  on equation (A4) gives

$$\begin{aligned} \mu(t) &= \int_{\alpha}^{\beta} ap(a, t) da = \int_{\alpha}^{\beta} a \frac{1}{\lambda_1(t) \left[ 1 - e^{-(\beta-\alpha)/\lambda_1(t)} \right]} e^{-(a-\alpha)/\lambda_1(t)} da \\ &= \frac{\alpha + \lambda_1(t) - (\beta + \lambda_1(t)) e^{-(\beta-\alpha)/\lambda_1(t)}}{1 - e^{-(\beta-\alpha)/\lambda_1(t)}}, \end{aligned}$$

from which

$$\begin{aligned} p(a, t) &= \frac{\beta + \lambda_1(t) - \mu(t)}{\lambda_1(t)(\beta - \alpha)} e^{-(a-\alpha)/\lambda_1(t)}, \quad \alpha \leq a \leq \beta, \quad \text{with} \\ \mu(t) &= \frac{\alpha + \lambda_1(t) - (\beta + \lambda_1(t)) e^{-(\beta-\alpha)/\lambda_1(t)}}{1 - e^{-(\beta-\alpha)/\lambda_1(t)}}. \end{aligned} \tag{A5}$$

Since  $p(a, t) = N(a, t)/N(t)$ ,

$$\begin{aligned} N(a, t) &= \frac{N(t) (\beta + \lambda_1(t) - \mu(t))}{\lambda_1(t)(\beta - \alpha)} e^{-(a-\alpha)/\lambda_1(t)}, \quad \alpha \leq a \leq \beta, \quad \text{with} \\ \mu(t) &= \frac{\alpha + \lambda_1(t) - (\beta + \lambda_1(t)) e^{-(\beta-\alpha)/\lambda_1(t)}}{1 - e^{-(\beta-\alpha)/\lambda_1(t)}}. \end{aligned} \tag{A6}$$

Differentiating  $N(a, t)$  with respect to  $a$  yields

$$\frac{\partial N(a, t)}{\partial a} = -\frac{1}{\lambda_1(t)} \frac{N(t) (\beta + \lambda_1(t) - \mu(t))}{\lambda_1(t)(\beta - \alpha)} e^{-(a-\alpha)/\lambda_1(t)} = -\frac{1}{\lambda_1(t)} N(a, t), \tag{A7}$$

or

$$-\frac{1}{N(a, t)} \frac{\partial N(a, t)}{\partial a} = \frac{1}{\lambda_1(t)}. \tag{A8}$$

Now, let us see what  $\lambda_1(t)$  means from

$$\mu(t) = \frac{\alpha + \lambda_1(t) - (\beta + \lambda_1(t)) e^{-(\beta-\alpha)/\lambda_1(t)}}{1 - e^{-(\beta-\alpha)/\lambda_1(t)}}.$$

If  $\beta \rightarrow \infty$ ,  $\lambda_1(t) = \mu(t) - \alpha$ ; if  $\beta \rightarrow \infty$  and  $\alpha = 0$ ,  $\lambda_1(t) = \mu(t)$ . So,  $\lambda_1(t)$  is indeed a measure of an animal's age, with an approximate value of  $\mu(t) - \alpha$  or  $\mu(t)$ ! Therefore,

$$-\frac{1}{N(a,t)} \frac{\partial N(a,t)}{\partial a} \frac{da}{dt} = \frac{1}{\lambda_1(t)} \frac{da}{dt} \approx \frac{1}{[\mu(t) - \alpha]} \frac{da}{dt} \approx \frac{1}{\mu(t)} \frac{da}{dt}. \quad (\text{A9})$$

If  $\frac{da}{dt} = 1$ , i.e., an individual's age changes at the same rate as time, equation (A9) becomes

$$-\frac{1}{N(a,t)} \frac{\partial N(a,t)}{\partial a} \frac{da}{dt} = \frac{1}{\lambda_1(t)} \approx \frac{1}{\mu(t) - \alpha} \approx \frac{1}{\mu(t)}. \quad (\text{A10})$$

## REFERENCES

1. S. Ohsumi, Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the southern hemisphere minke whale, *Rep. Int. Whaling Commission* **29** (2), 397-406, (1979).
2. D.R. Gunderson, Using  $r$ - $K$  selection theory to predict natural mortality, *Can. J. Fish. Aquat. Sci.* **37** (12), 2266-2271, (1980).
3. D. Pauly, On the relationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks, *J. Cons. Int. Explor. Mer.* **39** (2), 175-192, (1980).
4. J.M. Hoenig, Empirical use of longevity data to estimate mortality rates, *Fish. Bull. U.S.* **82** (1), 898-903, (1983).
5. D.R. Gunderson and P.H. Dygert, Reproductive effort as a predictor of natural mortality rate, *J. Cons. Int. Explor. Mer.* **44** (2), 200-209, (1988).
6. A.L. Jensen, Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival, *Can. J. Fish. Aquat. Sci.* **53** (4), 820-822, (1996).
7. T. Brey and J.D. Gage, Interactions of growth and mortality in benthic invertebrate populations: Empirical evidence for a mortality-growth continuum, *Arch. Fish. Mar. Res.* **45** (1), 45-59, (1997).
8. Y. Xiao, How does somatic growth rate affect otolith size in fishes?, *Can. J. Fish. Aquat. Sci.* **53** (7), 1675-1682, (1996).
9. J.S. Huxley, *Problems of Relative Growth*, 2<sup>nd</sup> Edition, Dover Publications, New York, (1972).
10. D.M. Bates and D.G. Watts, *Nonlinear Regression Analysis and Its Applications*, John Wiley and Sons, New York, (1988).
11. R.B. Evens, A new approach for deciding upon constraints in the maximum entropy formalism, In *The Maximum Entropy Formalism*, (Edited by R.D. Levine and M. Tribus), pp. 169-206, MIT Press, Cambridge, MA, (1978).