Formulae for calculating the instantaneous rate of natural mortality of animals from its surrogates

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Abstract Interspecific relationships between the instantaneous rate of natural mortality of fish in a natural population and its surrogates are useful for studies of their population dynamics. In this paper, I derive interspecific models for the instantaneous rate of natural mortality of animals in a natural population as a function of its age-, length- and mass-based surrogates, demonstrate their relationships with existing interspecific models, and fit them into data from three groups of animals. At equilibrium and for the most stable distribution of individuals of a population, the sum of the population's instantaneous rates of natural and fishing mortalities is in inverse proportion to the population's age-based surrogates (e.g., mean age, longevity, age at maturity and observed maximum age) and increases linearly with the rate of its individual's growth in length or mass.

1.1 Introduction

The instantaneous rate of natural mortality is a fundamental quantity of a natural population of animals and can be calculated from the number of deaths in the population over time. Unfortunately, in most cases, neither the time of death of an individual nor the number of deaths over time can be observed. Consequently, it can only be estimated from indirect information.

Many intraspecific and several interspecific models are available for this purpose. Interspecific models represent the instantaneous rate of natural mortality of an animal population as a function of its surrogates and provides a useful means for its calculation, especially in the absence of detailed intraspecific data (Ohsumi 1979; Gunderson 1980; Pauly 1980; Hoenig 1983; Gunderson and Dygert 1988; Jensen 1996; Brey and Gage, 1997). In this paper, I derive a new set of interspecific models, demonstrate their relationships with existing ones, and fit them into data from three groups of animals.

1.2 Model for $F(a,t) + M(a,t)$

Let $N(a,t) \geq 0$, $0 \leq a_0' \leq a < \infty$, $0 \leq t_0 \leq t < \infty$, 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 Δt is assumed to be proportional to $N(a,t)$, such that

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

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 $\Delta t \to 0$ give

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

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

from which

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

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

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

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

Now, both λ and μ 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

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

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

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

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

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

1.3 Age-based models

An age-based quantity T (e.g., age at maturity, longevity or observed maximum age) of a population of animals can be assumed, to the first approximation, to be in direct

proportion to its "equilibrial" age λ or mean age μ of its equilibrial population, i.e., $S(\lambda) = T \propto \lambda$, or

(7) $\quad S(\lambda) = T = \alpha\lambda$

with proportionality constant α. Substitution of equation 7 into equation 3 yields

(8) $\quad F(a,t) + M(a,t) = \alpha/T$

where α is the parameter to be estimated. In using an age-based model, it is important to choose an age-based quantity, such that α is constant across all species of interest.

Notice that equation 8 is equivalent in form to Ohsumi's (1979, p.401, lines 10-19) ($T = T$, $F(a,t) = 0$, $M(a,t) = M$ and $\alpha = \log(a)$), to Hoenig's (1983) equation 2 ($\alpha = -\log(k)$, $Z = F(a,t) + M(a,t)$ and $T = t_L$), and to Jensen's (1996) equation 7 ($F(a,t) = 0$, $\alpha = 1.65$ and $T = x_m$). Their equations were, however, obtained on different grounds. Ohsumi (1979) 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 (1983) defined it as the age to which an arbitrarily small proportion of a stock survive. Such arbitrariness seems to have left something to be desired. Finally, Jensen's (1996) 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. Alternatively, one can maximize their reproductive output in their life history

$$\int_{a_m}^{\infty} f(a)\,da \text{ to yield an average age at maturity } a_m = a_0'!$$

Thus, animals should mature as early as possible to maximize their reproductive output in their lives.

1.4 Length-based models

To relate the "equilibrial" age λ and mean age μ of an equilibrial population to a length-based quantity, 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

$$\dot{L} = K(L_\infty - L) \quad 0 \leq K,\ 0 \leq L \leq L_\infty,\ 0 \leq \dot{L} \leq KL_\infty,$$

$$\dot{L} = KL(1 - L/L_\infty) \quad 0 \leq K,\ 0 \leq L \leq L_\infty,\ 0 \leq \dot{L} \leq \tfrac{1}{4}KL_\infty, \quad \text{and}$$

$$\dot{L} = KL \log_e(L_\infty/L) \quad 0 \leq K,\ 0 \leq L \leq L_\infty,\ 0 \leq \dot{L} \leq \tfrac{1}{e}KL_\infty,$$

with von Bertalanffy, logistic or Gompertz parameters (K, L_∞). Note that K and L_∞ have exactly the same meaning in those equations: K is the growth rate of an individual animal; L_∞ 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 (Xiao 1996),

$$L(a) = L_\infty - [L_\infty - L(a_0)]e^{-K(t-a_0)},$$

$$L(a) = \frac{L(a_0)L_\infty}{L(a_0) + [L_\infty - L(a_0)]e^{-K(t-a_0)}} \quad \text{and}$$

$$L(a) = L_\infty [L(a_0)/L_\infty]^{e^{-K(t-a_0)}}.$$

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

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

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

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

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

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

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

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

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, in which case equations 10.1-10.3 all become

$$(11) \quad F(a,t) + M(a,t) = K/\beta$$

but with parameter

$$\beta = Ka_0 - \log\left(\frac{L_\infty - L(\lambda)}{L_\infty - L(a_0)}\right),$$

$$\beta = Ka_0 - \log\left(\frac{L(a_0)[L_\infty - L(\lambda)]}{L(\lambda)[L_\infty - L(a_0)]}\right) \quad \text{and}$$

$$\beta = Ka_0 - \log\left(\frac{\log(L_\infty/L(\lambda))}{\log(L_\infty/L(a_0))}\right).$$

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 β is constant across all species concerned. Clearly, equation 11 has the same functional form as Jensen's (1996) equation 8, which was, however, derived under a restrictive assumption (see above).

1.5 Mass-based models through length

To relate the "equilibrial" age λ and mean age μ of an equilibrial 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

$$(12) \quad S(a) = c' + a'L(a)^{b'} \quad \text{(Huxley 1972) or}$$

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

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 $c'\leq0$. Substitution of equation 13 for $a=\lambda$ into equation 11 yields

$$(14) \quad F(a,t)+M(a,t)=K/\gamma$$

with parameter

$$\gamma = Ka_0 - \log\left(\frac{L_\infty - \left(\frac{S(\lambda)-c'}{a'}\right)^{-b'}}{L_\infty - L(a_0)}\right),$$

$$\gamma = Ka_0 - \log\left(\frac{L(a_0)\left[L_\infty - \left(\frac{S(\lambda)-c'}{a'}\right)^{-b'}\right]}{L(\lambda)\left[L_\infty - L(a_0)\right]}\right) \quad \text{and}$$

$$\gamma = Ka_0 - \log\left(\frac{\log\left(L_\infty\left(\frac{S(\lambda)-c'}{a'}\right)^{b'}\right)}{\log(L_\infty/L(a_0))}\right).$$

Similarly, models alternative to Gunderson's (1980) and Gunderson and Dygert's (1988) 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.

1.6 Data and analysis

Use of equation 8 to estimate α requires data on $F(a,t)$, $M(a,t)$ and T; use of equation 11 to estimate β requires data on $F(a,t)$, $M(a,t)$ and K. However, 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.

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 (1979) data on the instantaneous rate of mortality $M(a,t)$ of cetaceans as a function of their fishing mortality $F(a,t)$ and observed maximum age T, under the assumption that the errors in $M(a,t)$ are independent, identical normal variates, yields $\hat{F}(a,t)$=-0.0062 (±0.0063) ·yr^{-1}, $\hat{\alpha}$=5.1144 (±0.3693), $F_{2,17}$=611.2678, P=0.0001, r^2=0.9863, n=19. 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. So, fitting of equation 8 to the same data on the instantaneous rate of mortality $M(a,t)$ of cetaceans as a function of their observed maximum age T, under the assumptions that $F(a,t)$=0 and the errors in $M(a,t)$ are independent, identical normal variates, yields $\hat{\alpha}$=4.7725 (±0.1365), $F_{1,18}$=1222.0446, P=0.0001, r^2=0.9855, n=19. Notice that, in both 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.

Fitting of equation 11 to Gunderson and Dygert's (1988) data on the instantaneous rate of mortality $M(a,t)$ of fish 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, identical normal variates, yields $\hat{F}(a,t)$=0.0652 (±0.1246) ·yr^{-1}, $\frac{\hat{1}}{\beta}$=1.0632 (±0.4453), $F_{1,18}$=5.700, P=0.0281, r^2=0.2405, n=20. 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 mortality $M(a,t)$ of fish as a function of growth rate K, under the assumptions that $F(a,t)$=0 and the errors in $M(a,t)$ are independent, identical normal variates, yields $\frac{\hat{1}}{\beta}$=1.2718 (±0.1944), $F_{1,19}$=42.8242, P=0.0001, r^2=0.6927, n=20.

Fitting of equation 11 to Brey and Gage's (1997) data on the instantaneous rate of mortality $M(a,t)$ of fish 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, identical normal variates, yields $\hat{F}(a,t)$=-0.1077 (±0.1251) ·yr^{-1}, $\frac{\hat{1}}{\beta}$=2.5709 (±0.1629), $F_{1,80}$=249.2049, P=0.0001, r^2=0.7570, n=82. Similarly, fitting of equation 11 to these data on the instantaneous rate of mortality $M(a,t)$ of fish as a function of growth rate K, under the assumptions that $F(a,t)$=0 and the errors in $M(a,t)$ are independent, identical normal variates, yields $\frac{\hat{1}}{\beta}$=2.4825 (±0.1262), $F_{1,81}$=386.6960, P=0.0001, r^2=0.8268, n=82.

1.7 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 great 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, 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 propagation to parameters.

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 (1988) data and Brey and Gage's (1997) data very well.

1.8 Acknowledgments

1.9 References

Brey, T., 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, 45-59, 1997.

Evens, R.B., 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, Mass., 1978.

Gunderson, D.R., Using r-K selection theory to predict natural mortality. Can. J. Fish. Aquat. Sci., 37, 2266-2271, 1980

Gunderson, D.R., and P.H. Dygert, Reproductive effort as a predictor of natural mortality rate. J. Cons. Int. Explor. Mer, 44, 200-209, 1988.

Hoenig, J.M., Empirical use of longevity data to estimate mortality rates. Fish. Bull. U.S., 82, 898-903, 1983.

Huxley, J.S., Problems of relative growth. 2nd Edition. Dover Publications, Inc., 312 p., New York, 1972

Jensen, A.L., Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can. J. Fish. Aquat. Sci., 53, 820-822, 1996.

Ohsumi, S., 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, 397-406, 1979.

Pauly, D., On the relationship between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer, 39, 175-192, 1980

Xiao, Y., How does somatic growth rate affect otolith size in fishes? Can. J. Fish. Aquat. Sci., 53, 1675-1682, 1996.

Appendix A Derivation of equation 3

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

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

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

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

under the constraints that

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

where $p(a,t) = N(a,t)/N(t)$. These constraints are, of course, justified mathematically (Evens 1978). To solve this variation problem, let

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

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

$$\frac{\partial H}{\partial p(a,t)} = -[\log(p(a,t)) + 1] + \lambda_0(t) - \frac{a}{\lambda_1(t)} = 0 \text{ yield}$$

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

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 $\frac{\partial^2 H}{\partial p(a,t)^2} = -1/p(a,t) < 0$. Substitution of equation A3 into the constraint $1 = \int_{\alpha}^{\beta} p(a,t) da$ gives

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

from which

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

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

$$\mu(t) = \int_{\alpha}^{\beta} a p(a,t) da = \int_{\alpha}^{\beta} a \frac{1}{\lambda_1(t)[1 - e^{-(\beta - \alpha)\lambda_1(t)}]} e^{-(a - \alpha)/\lambda_1(t)} da = \frac{\alpha + \lambda_1(t) - (\beta + \lambda_1(t)) e^{-(\beta - \alpha)\lambda_1(t)}}{1 - e^{-(\beta - \alpha)\lambda_1(t)}}$$

from which

$$(A5) \quad p(a,t) = \frac{\beta + \lambda_1(t) - \mu(t)}{\lambda_1(t)(\beta - \alpha)} e^{-(a - \alpha)/\lambda_1(t)} \quad \alpha \leq a \leq \beta, \quad \text{with}$$

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

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

$$(A6) \quad N(a,t) = \frac{N(t)(\beta + \lambda_1(t) - \mu(t))}{\lambda_1(t)(\beta - \alpha)} e^{-(a - \alpha)/\lambda_1(t)} \quad \alpha \leq a \leq \beta \quad \text{with}$$

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

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

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

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

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

$$\mu(t) = \frac{\alpha + \lambda_1(t) - (\beta + \lambda_1(t)) e^{-(\beta - \alpha)/\lambda_1(t)}}{1 - e^{-(\beta - \alpha)/\lambda_1(t)}}: \text{ if } \beta \to \infty, \lambda_1(t) = \mu(t) - \alpha; \text{ if}$$

$\beta \to \infty$ 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,

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

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

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