# Empirical Use of Longevity Data to Estimate Mortality Rates

J.M. Hoenig

# SEDAR33-RD17

3 April 2013

Please cite as:

Hoenig, J.M. 2005. Empirical Use of Longevity Data to Estimate Mortality Rates. SEDAR33-RD17. SEDAR, North Charleston, SC. 8 pp.

# EMPIRICAL USE OF LONGEVITY DATA TO ESTIMATE MORTALITY RATES

Various investigators have utilized compendia of life history parameters to develop equations for predicting values of difficult-to-estimate parameters from easily measured or estimated quantities. For example, Pauly (1979) developed multiple regressions to predict the natural mortality rate of fish from growth parameters and mean water temperature. Ohsumi (1979) developed linear regressions for estimating natural mortality of cetaceans from maximum length or maximum age. In this paper, a general regression equation is developed to predict the total mortality rate of fish, cetacean, and mollusk stocks from the maximum age.

It seems intuitive that longevity and mortality rate in a species should be inversely related since animals from a population with a high mortality rate would not survive long enough to reach old age. The nature of the relationship between mortality and maximum age is explored below.

FISHERY BULLETIN: VOL. 82, NO. 1, 1983.

## Development of the Model

In fishery biology, it is generally assumed that, after some early life history stages, the mortality rate is constant. That is, the proportion reaching age $t$ is given by

$$\frac{N_t}{N_0} = e^{-Zt} \qquad (1)$$

where $Z$ is the constant instantaneous rate of mortality, $N_t$ is the number surviving to age $t$, and $N_0$ is the initial number present so that $N/N_0$ is the proportion surviving to age $t$.

Suppose the longevity of a stock is defined as the age, $t_L$, to which a proportion, $k$, of the animals survive, where $k$ is some arbitrarily small constant (e.g., 0.01). Then

$$k = e^{-Zt_L}$$

and

$$\ln(k) = -Zt_L. \qquad (2)$$

Equation (2) describes a hyperbola which can be linearized by plotting the mortality rate against $1/t_L$ or by plotting log $(Z)$ against log $(t_L)$.

In Equation (2), $t_L$ is a quantile that is determined by aging the fish in the upper tail of a length-frequency sample. However, it is considerably easier to find the maximum age, $t_{\max}$, in a sample (by aging just the largest few fish) than it is to estimate a quantile. Thus, it is of interest to know if Equation (2) will hold, at least approximately when $t_{\max}$ is substituted for $t_L$.

Tanaka (1960) plotted the mortality rate versus $1/t_{\max}$ for five fish species and suggested that the apparently linear relationship deserves further investigation. Beverton (1963) and Bayliff (1967) made the same kind of plot for fishes in the families Clupeidae and Engraulidae, and Ohsumi (1979) investigated the situation within the Cetacea.

In this paper, plots of log (mortality) versus log $(t_{\max})$ were investigated for three taxonomic groups comprising 134 stocks.

## Data and Results

Data on the total mortality rates and the corresponding maximum observed ages were taken mainly from the compendia by Beverton and Holt (1959), Ohsumi (1979), and McBride and Brown (1980). Most of the data pertain to unexploited or lightly exploited stocks. All of the data are shown in Figure 1 and their sources are listed in Hoenig (1982). The data for the mollusks are shown separately in Figure 2.

Results of calculating ordinary least squares linear regressions on the log transformed data are given in the following table:

| *Taxonomic* | *Sample size* | | *Slope* | *Intercept* | | | |
|---|---|---|---|---|---|---|---|
| *group* | *Stocks* | *Species* | b | a | $r^2$ | F | *df* |
| Mollusks | 28 | 13 | −0.832 | 1.23 | 0.78 | 91 | 1,26 |
| Fish | 84 | 53 | −1.01 | 1.46 | 0.68 | 177 | 1,82 |
| Cetaceans | 22 | 13 | −0.873 | 0.941 | 0.70 | 47 | 1,20 |
| All | 134 | 79 | −0.982 | 1.44 | 0.82 | 595 | 1,132 |

The predictive equations are of the form

$$\ln(Z) = a + b \ln(t_{\max}).$$

The four regression lines are very similar. The combined regression equation makes use of data over the widest possible range of ages (1-123 yr) and has the highest coefficient of determination ($r^2$). It is suggested that the combined regression equation be used for predictive purposes for all three groups.

## Discussion

The high values of the coefficients of determination in the above regressions indicate that the equations have considerable predictive power. The relationship between mortality rate and maximum age appears to hold within a species as well. This is demonstrated by the data for 10 stocks of Pacific razor clam, *Siliqua patula*, and 6 stocks of Nuttall's cockle, *Clinocardium nuttallii*, shown in Figure 2.

In deriving the regression approach, it was assumed that the mortality rate does not vary with age. However, it is well known that in at least some groups of fish (e.g., sturgeons, Ricker 1975: ch. 2; clupeids and engraulids, Beverton 1963; and salmonids, Gerking 1957) the mortality rate appears to increase with age. Concave catch curves, suggestive of decreasing mortality rate with age, have sometimes been reported but these have usually been given other interpretations (Ricker 1975: ch. 2). In general, not much is known about the mortality rates among the oldest animals of most species (and how mortality might vary among taxa).

The regressions presented here are based largely on data from unexploited stocks. Since the scatter plots and regression statistics indicate a strong linear relationship between the maximum age and the mortality rate, the method works well for predicting mortality rates in unexploited stocks. If age truncation is a common phenomenon among the stocks for which data were available, then the application of this technique to heavily exploited stocks may result in an underestimate of the mortality rate.

## Applications

The regression technique can be used in several distinct applications:

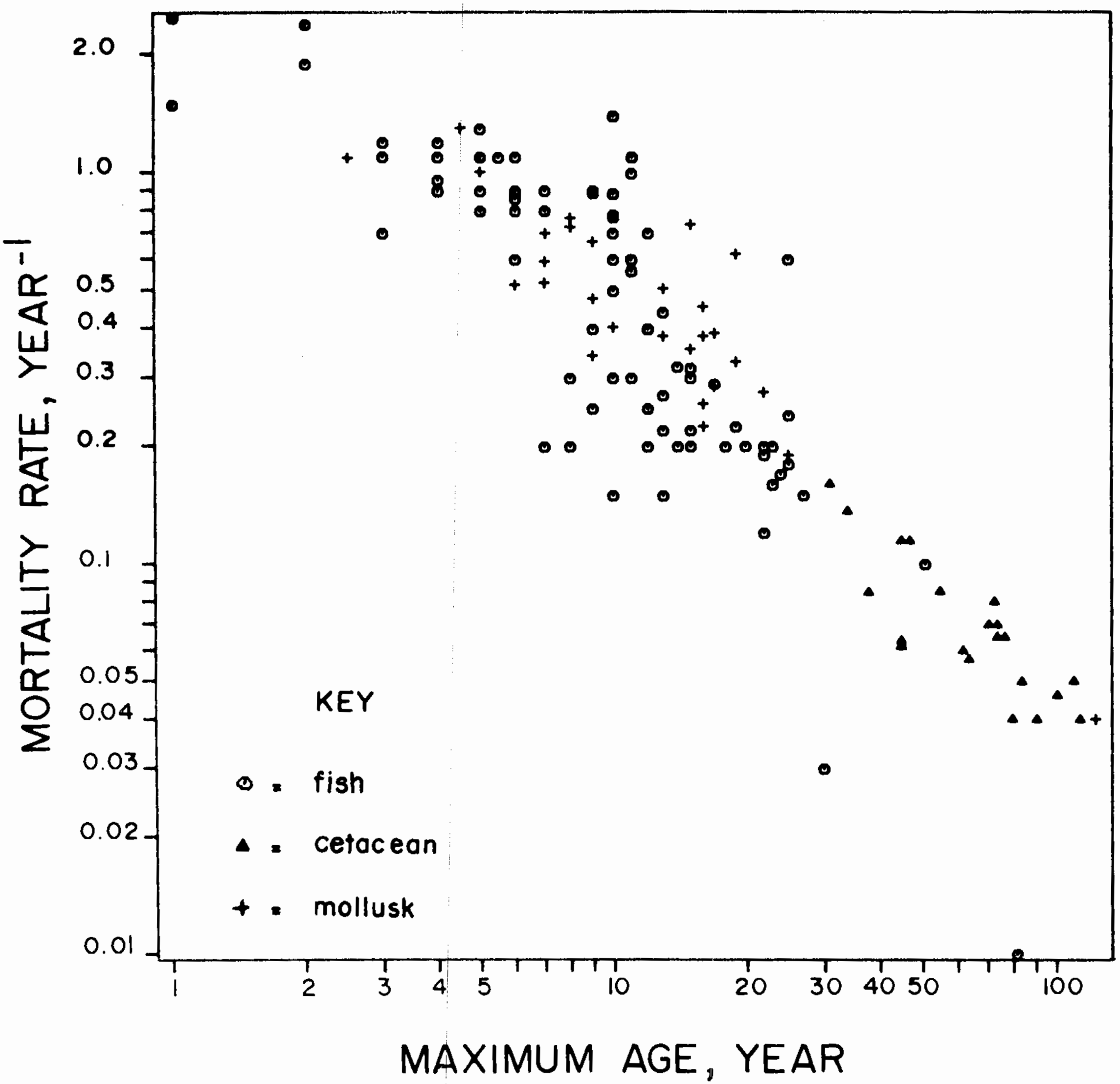

FIGURE 1.—Plot of instantaneous mortality rate ($yr^{-1}$) against maximum observed age (yr), both on logarithmic scales.

1) A quick preliminary estimate of the mortality rate can be obtained by aging just the largest few fish. This does not preclude aging the rest of the sample at a later date.

2) In some cases, the number of age determinations must be kept to a minimum because of time or cost constraints; e.g., determining the ages of tropical fishes may necessitate a tedious procedure of counting daily growth rings (Brothers 1980; Brothers et al. 1976).

3) The procedure can be used when the sample is not representative of the population. This can occur as the result of a particular sampling scheme or if the animals segregate by size.

4) An interesting application of the method is to cases where recruitment is highly variable. In an extreme case, Goldspink (1981) reported finding only three or four year classes in bream, *Abramis brama*, in three English lakes even though the maximum age found was 23 yr. A maximum age of 23 yr would normally indicate a mortality rate of 0.19. However, this is likely to be a maximal estimate, since older fish might have been found if there had happened to be a strong year class in an earlier year.

5) The technique can also be used to obtain a rough estimate of the mortality rate when the maximum age

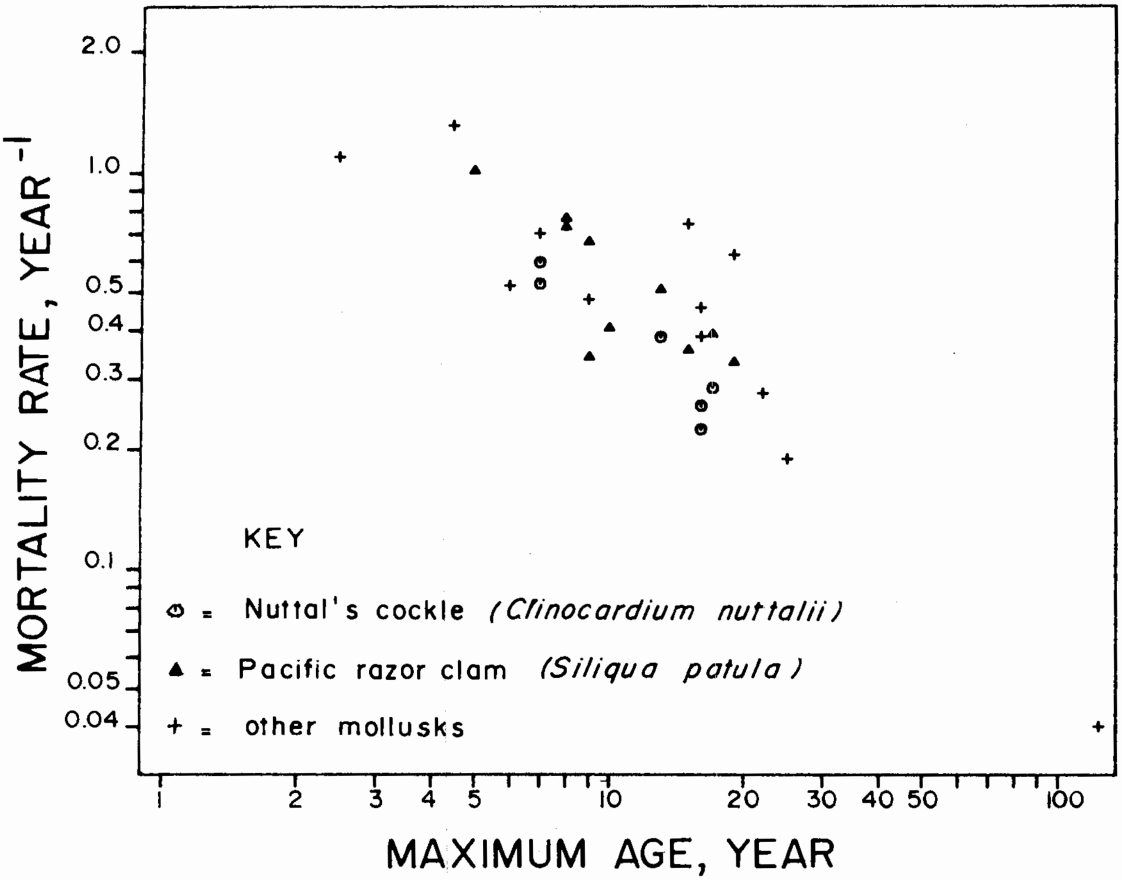

FIGURE 2.—Plot of instantaneous mortality rate (yr$^{-1}$) against maximum observed age (yr), both on logarithmic scales, for 28 stocks of mollusks.

is the only information available; e.g., McBride and Brown (1980) summarized the life history parameters of the major fish stocks in the western North Atlantic. For the following species McBride and Brown gave estimates of maximum age but not of natural mortality rates. The estimates provided here were calculated by the regression method.

| *Species* | *Max. age (yr)* | *Predicted* M (yr$^{-1}$) |
|---|---|---|
| Ocean pout, *Macrozoarces americanus* | 18 | 0.25 |
| Scup, *Stenotomus chrysops* | 19 | 0.23 |
| Black sea bass, *Centropristis striatus* | 20 | 0.22 |
| White hake, *Urophycis tenuis* | 23 | 0.19 |
| Bull shark, *Carcharhinus leucas*[1] | 28 | 0.16 |
| Dusky shark, *Carcharhinus obscurus*[1] | 30 | 0.15 |
| Angler, *Lophius americanus* | 30 | 0.15 |
| Tilefish, *Lopholatilus chamaeleonticeps* | 40-50 | 0.11-0.09 |

The major limitation of the technique is that the sample size is not taken into consideration. The maximum age observed depends on the number of animals in the sample since rare, old animals are more likely to be found in large samples. However, once a sample of, say, 200 animals has been examined, the maximum age tends to increase slowly with increasing sample size. The nature of the relationship between sample size and maximum age is examined in Appendix A. Because the sample size is not taken into consideration, it is not possible to attach confidence bounds to the estimates or to test hypotheses.

Another limitation is that the age structure will change slowly following a decrease in the mortality rate. Hence, the maximum age will remain depressed for several years resulting in an overestimate.

This regression technique appears to have considerable predictive power for estimating mortality. It is useful in a variety of situations where the data are limited. However, the statistical foundation underlying the technique is weak thus precluding the making

---

[1] Maximum ages for the sharks were taken from the growth study by Hoenig (1979). The estimates are believed to be conservative.

of critical comparisons. More sophisticated statistical methods, which implicitly take the sample size into consideration but which require stronger adherence to the assumptions of the exponential model, are discussed in Hoenig and Lawing (1982) and Hoenig (1983).

## Acknowledgments

Saul Saila, William Lawing, and Michael Sissenwine made helpful comments on an earlier draft of this manuscript. Malcolm Champlin suggested the approximation in Appendix A. Susan Clements-Proulx and Pat Aldrich typed the manuscript. I would also like to thank Lynn Goodwin for generously providing unpublished data on the geoduck clam. The anonymous reviewers made helpful comments.

## Literature Cited

BAYLIFF, W. H.

1967. Growth, mortality, and exploitation of the Engraulidae with special reference to the anchoveta, *Cetengraulis mysticetus*, and the colorado, *Anchoa naso*, in the eastern Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 12:365-432.

BEVERTON, R. J. H.

1963. Maturation, growth and mortality of Clupeid and Engraulid stocks in relation to fishing. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 154:44-67.

BEVERTON, R. J. H., AND S. J. HOLT.

1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Ciba Found. Colloq. Ageing 5:142-177.

BROTHERS, E. B.

1980. Age and growth studies on tropical fishes. *In* S. B. Saila and P. M. Roedel (editors), Stock assessment for tropical small-scale fisheries, p. 119-136. Int. Cen. Mar. Res. Dev., Univ. Rhode Island, Kingston, 198 p.

BROTHERS, E. B., C. P. MATTHEWS, AND R. LASKER.

1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.

GERKING, S. D.

1957. Evidence of aging in natural populations of fishes. Gerontology 1(5):287-305.

GOLDSPINK, C. R.

1981. A note on the growth-rate and year-class strength of bream, *Abramis brama* (L.), in three eutrophic lakes, England. J. Fish Biol. 19:665-673.

HOENIG, J. M.

1979. The vertebral centra of sharks and their use in age determination. M.S. Thesis, Univ. Rhode Island, Kingston, 144 p.

1982. A compilation of mortality and longevity estimates for fish, mollusks and cetaceans with a bibliography of comparative life history studies. Univ. Rhode Island, Grad. School Oceanogr. Tech. Rep., Ref. 82-2, 14 p.

1983. Estimating total mortality rate from longevity data. Ph.D. Thesis, Univ. Rhode Island, Kingston.

HOENIG, J. M., AND W. D. LAWING.

1982. Estimating the total mortality rate using the maximum order statistic for age. Int. Counc. Explor. Sea C. M. 1982/D:7, 13 p.

HOLT, S. J.

1965. A note on the relation between the mortality rate and the duration of life in an exploited fish population. Int. Comm. Northwest Atl. Fish. Res. Bull. 2:73-75.

JOHNSON, N. L., AND S. KOTZ.

1970. Continuous univariate distributions-1. John Wiley & Sons, N.Y., 300 p.

MCBRIDE, M. M., AND B. E. BROWN.

1980. The status of the marine fishery resources of the northeastern United States. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/NEC-5, 29 p.

OHSUMI, S.

1979. Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the southern hemisphere minke whale. Rep. Int. Whaling Comm. 29:397-406.

PAULY, D.

1979. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer 39:175-192.

RICKER, W. E.

1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

TANAKA, S.

1960. Studies on the dynamics and management of fish populations. [In Jpn.] Bull. Tokai Reg. Fish. Res. Lab. 28:1-200.

JOHN M. HOENIG

*University of Rhode Island*
*Graduate School of Oceanography*
*Narragansett, RI* 02882-1197
Present address: *Minnesota Department of Natural Resources*
*Section of Fisheries*
*Box 12, Centennial Office Building*
*St. Paul, MN 55155*

# APPENDIX A

## Relationship Between Maximum Observed Age and Sample Size

Assume that life duration follows a two-parameter exponential distribution with probability density function

$$f(t) = Ze^{-Z(t-t_c)}$$

where $Z$ is the instantaneous mortality rate, $t$ is age, and $t_c$ is the youngest age fully represented in the catch. Also assume a stable age distribution (i.e., that recruitment is continuous and constant). Under these restrictive conditions, the expected value of the maximum age in a sample of size $n$ is given by (Johnson and Kotz 1970: 216)

$$E(t_{\max}) = \frac{1}{Z} \sum_{i=1}^{n} \frac{1}{i} + t_c. \tag{1}$$

To see the effect of sample size on the maximum age more clearly, we can approximate Equation (1) by

$$\frac{1}{Z}\sum_{i=1}^{n}\frac{1}{i}+t_c \cong \frac{1}{Z}\int_{1/2}^{n+1/2}\frac{dX}{X}+t_c=\frac{\ln(2n+1)}{Z}+t_c.$$

Hence $$E(t_{\max}) \cong \frac{\ln(2n+1)}{Z}+t_c. \qquad (2)$$

Holt (1965) presented similar findings as an asymptotic result.

The expected value of the maximum age is shown in the table for three values of $Z$ and several values of $n$ when $t_c$ equals 0.

$$E(t_{\max}) = \frac{1}{Z}\sum_{i=1}^{n}\frac{1}{i} \text{ for } Z =$$

| $n$ | 1.0 | 0.5 | 0.25 |
|---|---|---|---|
| 50 | 4.5 | 9.0 | 18.0 |
| 100 | 5.2 | 10.4 | 20.7 |
| 150 | 5.6 | 11.2 | 22.4 |
| 200 | 5.9 | 11.8 | 23.5 |
| 250 | 6.1 | 12.2 | 24.4 |
| 500 | 6.8 | 13.6 | 27.2 |
| 1,000 | 7.5 | 15.0 | 29.9 |

Increasing the sample size from 100 to 1,000 causes the expected value of the maximum age to increase by 43%. Increasing the sample size from 200 to 1,000 will cause a 27% increase.

If the mortality rate is higher for older fish, the maximum age will increase even more slowly with increasing sample size. For example, if the age structure is governed by the Gompertz equation, the maximum age in a sample tends to increase as the log of the log of the sample size (Beverton 1963).

## Addendum

Dr. W. E. Ricker (pers. commun.) has suggested that a geometric mean (GM) regression would be more appropriate than the ordinary predictive (arithmetic mean, AM) regression for predicting values of log $Z$ since both variables are naturally variable. The regression equation presented here can be converted to a GM line by dividing the slope ($b$) by the square root of the coefficient of determination ($|r|$) and passing the line through the point defined by the means of the log transformed values of $Z$ and $t_{\max}$ (Ricker 1973). The means are: for mollusks, mean ($\ln(Z)$) $= -0.821$ and mean ($\ln(t_{\max})$) $= 2.465$; for fish, $-0.767$ and 2.214; for cetaceans, $-2.684$ and 4.154; for all groups, $-1.093$ and 2.585.