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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.

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

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

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

$$\ln(k) = -Zt_L \quad (2)$$

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 $\log(\text{mortality})$ 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 group	Sample size		Slope b	Intercept a	r ²	F	df
	Stocks	Species					
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, *Clino-cardium 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:

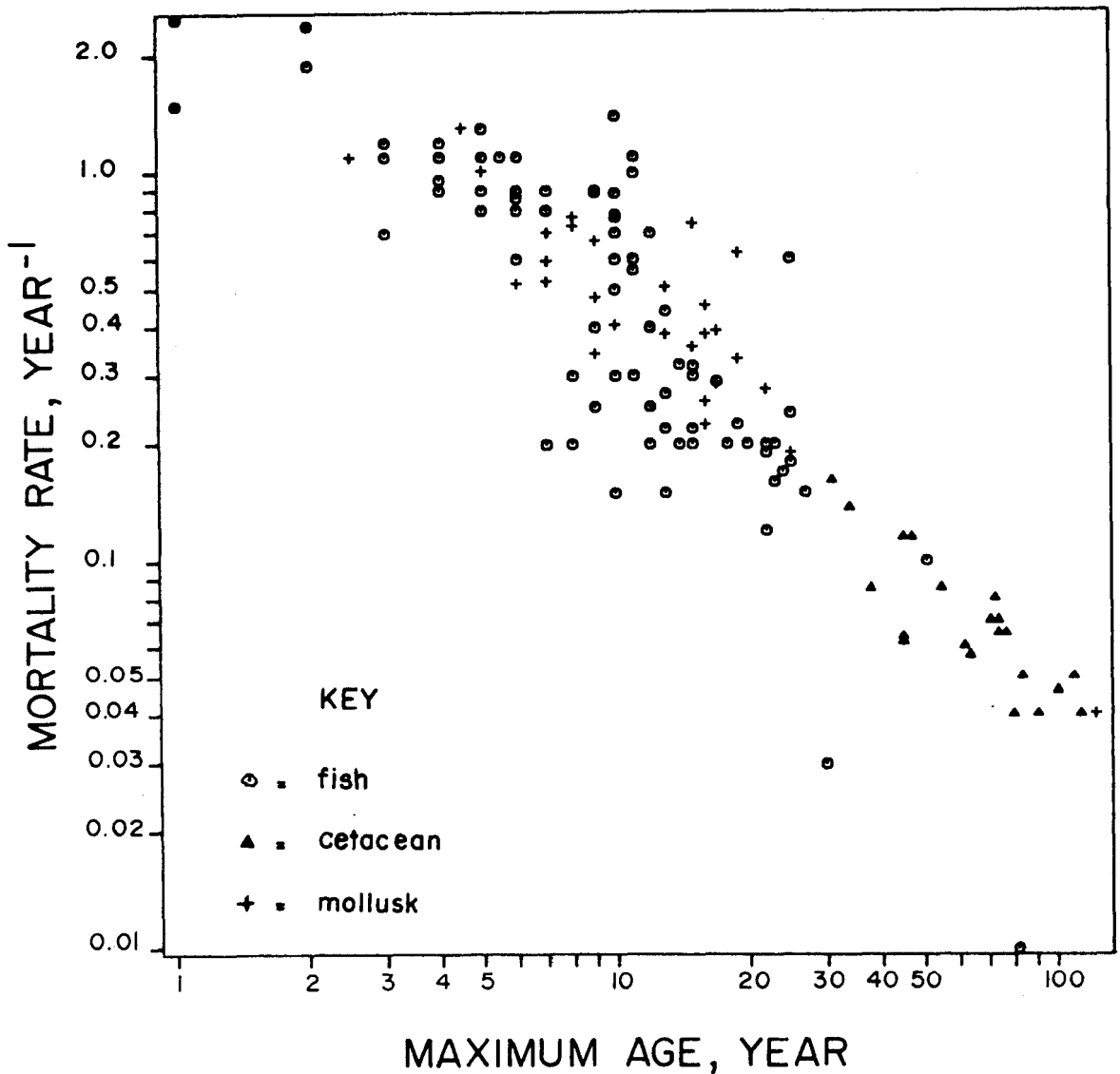


FIGURE 1.—Plot of instantaneous mortality rate (yr^{-1}) against maximum observed age (yr), both on logarithmic scales.

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

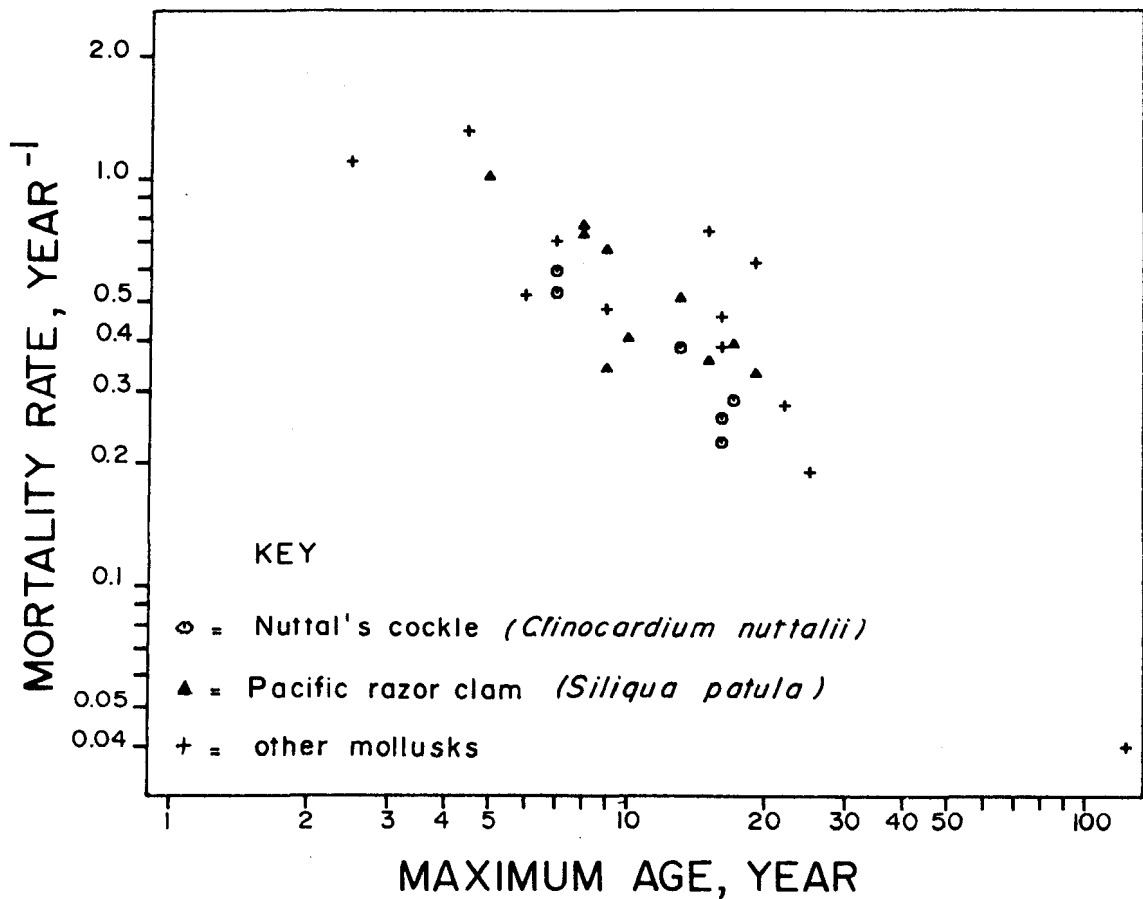


FIGURE 2.—Plot of instantaneous mortality rate (yr^{-1}) against maximum observed age (yr), both on logarithmic scales, for 28 stocks of mollusks.

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, <i>Macrozoarces americanus</i>	18	0.25
Scup, <i>Stenotomus chrysops</i>	19	0.23
Black sea bass, <i>Centropristis striatus</i>	20	0.22
White hake, <i>Urophycis tenuis</i>	23	0.19
Bull shark, <i>Carcharhinus leucas</i> ¹	28	0.16
Dusky shark, <i>Carcharhinus obscurus</i> ¹	30	0.15
Angler, <i>Lophius americanus</i>	30	0.15
Tilefish, <i>Lopholatilus chamaeleonticeps</i>	40-50	0.11-0.09

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

The major limitation of the technique is that the sample size is not taken into consideration. The max-

imum 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

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).

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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)

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

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

GROWTH OF *GERYON QUINQUEDENS* (BRACHYURA: GERYONIDAE) JUVENILES IN THE LABORATORY¹

The deep-sea red crab, *Geryon quinquegens* Smith, is a large brachyuran of commercial interest inhabiting the upper continental slope in the western Atlantic Ocean from Nova Scotia to Argentina (Scelzo and Valentini 1974). Studies of the biology of the species have concerned distribution, abundance, and bathymetric limits (Wigley et al. 1975; Haefner 1978); the ovarian cycle of adult females (Haefner 1977); and development and behavior of larvae in the laboratory (Perkins 1973; Rosowski 1979; Sulkin and Van Heukelem 1980; Kelly et al. 1982). Studies of the rate of growth of the species have been limited to inferential analysis of size-frequency data, and it appears that 13-15 molts are required for the crab to grow from a carapace width of 20 mm to the maximum size of 150 mm (Haefner 1978).

In this note we report results of a study of the effects of temperature on the rate of growth of juvenile red crabs in the laboratory.

Methods

Groups of juvenile red crabs were reared for nearly 1 yr at one of four temperatures: 6°, 9°, 12°, and 15°C. Temperatures were chosen to approximate those of bottom water at depths ranging from 200 to 2,000 m in the western North Atlantic (Haefner 1978). Each group at 6°, 9°, and 12°C consisted of five individuals. The crabs in these groups were the progeny of one female and resulted from laboratory-reared larvae. The group at 15° consisted of 25 crabs. These crabs were the progeny of another female whose larvae were also laboratory-reared.

During the experiment, juvenile red crabs were held in darkness at ambient pressure at 35‰ salinity. Diet consisted of frozen brine shrimp (*Artemia salina*), chopped mussel (*Mytilus edulis*), and clam (*Mercenaria mercenaria*), and bits of muscle from adult red crabs. Juveniles used in the experiment were subjected to experimental conditions upon molting from the megalopa stage to crab stage 1.

Crabs in groups at 6°, 9°, and 12°C were maintained individually in glass bowls (10.5 cm diameter) with a shallow layer of sand and a small piece of plastic tubing in which the crabs generally took up residence. The bowls were kept in aerated aquaria containing 25 l of filtered seawater. Upon molting to crab stage 4,

¹Contribution No. 1425 from the Center for Environmental Studies, University of Maryland, Cambridge, Md.