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A discussion of the potential use in population dynamics of the interrelationships between natural mortality, growth parameters and mean environmental temperature in 122 fish stocks.

by

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Abstract

A compilation of values for the exponential coefficient of natural mortality (M) is given for 122 different stocks of fish distributed in 84 species, both limnic and marine, and ranging from polar to tropical waters. Values of L_∞ (LT, cm), W_∞ (g, fresh weight), K (1/year) and T (°C, mean annual water temperature) were attributed to each value of M, and the 122 sets of values plotted such that:

1) $\log M = 0.1228 - 0.1912 \log L_\infty + 0.7485 \log K + 0.2391 \log T$

and

2) $\log M = -0.1091 - 0.1017 \log W_\infty + 0.5912 \log K + 0.3598 \log T$

The multiple correlation coefficient is for 1), 0.817 and for 2), 0.800, while the critical value (118 d.F.) is 0.303 at the 99% confidence level. All slopes are significantly $\neq 0$. The standard deviation of estimates of logM is for 1), 0.2656 and for 2), 0.2766. A discussion is given of the significance of these findings.

A quick technique is presented, in an addendum, for the estimation of values of the catchability coefficient (q) when M and only one value of Z (with corresponding value of effort) are known.

Introduction

The exponential coefficient of natural mortality (M) certainly is one of the parameters of which it is most difficult to obtain good estimates. On the other hand, values of this parameters are needed for most of the models presently used in fish population dynamics.
Natural mortality, as defined in the literature, is caused by all possible causes of death except by fishing. Direct estimates of M can therefore be obtained only from completely unfished stocks.

In exploited fish stocks, values of M may be obtained from values of total mortality (Z) minus fishing mortality (F) or by a plot of Z against contemporary effort data, M being the y-intercept (at f=0). (See RICKER, 1975 for discussion and definitions)

These two approaches obviously have their limitations, the first in the fact that most fish stocks are presently ± exploited, the second in the fact that total mortality and contemporary effort data are very often unavailable.

A third, comparative approach was therefore explored by various authors (starting with BEVERTON & HOLT, 1959) who attempted to relate M to some easy-to-estimate parameter, whose value could then be used to predict M.

Among the various parameters, it appeared quite early that M is closely related to the growth parameters of a given stock, especially to the parameter K of the VON BERTALANFFY growth formula (VBGF), which has the form:

$$Lt = L_{\infty} (1 - e^{-K(t - t_o)}) \qquad ....1)$$

for length, and

$$Wt = W_{\infty} (1 - e^{-K(t - t_o)})^3 \qquad ....2)$$

for weight. For brevity's sake, L_{∞} and W_{∞},the asymtotic length and weight respectively, will be referred to as "size" (S) wherever possible. The estimation of value for the growth parameters S and K to date represents no problem, and decent values of these parameters have been calculated for most large, exploited marine fish stocks of the world (See PAULY, 1978 for a compilation of original and literature values of L_{∞} and K values covering 1 500 different stocks distributed in over 500 species).

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There are still problems, however, in the definition of these parameters S and K. Pending a comprehensive account on the theory of fish growth (PAULY, in prep.) the parameters S and K may be defined as follows:

1) The asymptotic size (S) is about equal to the mean size the fish of a given stock would reach if they were to grow to a very old age. (PAULY, 1978).

2) The difinition of K causes more problems. VON BERTALANFFY (1951) assumed the anabolism of fishes to be proportional to the 2/3 power of weight, and the catabolism to be proportional to weight itself. It has since been shown, however, that the anabolism of fishes increases in proportion to a power of weight of about 0.8 (See WINBERG, 1956). The VON BERTALANFFY growth formula (VBGF) in the form given by BEVERTON & HOLT (1951) is, therefore, not a "physiological" formula, but rather an empirical formula, whose parameters are, however, of great heuristic value. An exhaustive discussion of the respective merits and demerits of the special VBGF (that is, of the VBGF in the formulation of BEVERTON & HOLT, 1957) and of the generalized VBGF (that is, of the four-parameters VBGF developed by RICHARD 1959, TAYLOR 1962, or URSIN 1967) will be given elsewhere (PAULY, in prep.). Suffice it here to point out the fact that the parameter K, even when given no physiological interpretation, still has the tendency to increase with all factors causing "stress" (that is, with all factors causing an increase of O_2 consumption) such as, for example, increasing temperatures. For this reason, the magnitude of K has a direct relationship with the longevity of any fish. This becomes obvious if we consider the feature, previously reported by TAYLOR (1958), BEVERTON (1963) and others, that the oldest fishes in a given unexploited stock in nature (not in the aquarium!) generally reach about 95% of their asymtotic length. So it is possible to estimate, for any value of L_∞, an approximate value for longevity (T_{max}). From the VBGF:

$$L_t = L_\infty \left(1 - e^{-K(t - t_o)}\right) \qquad \ldots.1)$$

it follows that

$$t - t_o = \frac{l_n \left(1 - \frac{l_{max}}{l_\infty}\right)}{-K} \qquad \ldots.3)$$

or, if we insert 95% of L_∞ for L_{max}

$$t - t_o = \frac{2.9957}{K} = \frac{3}{K} \qquad \ldots.4)$$

thus, $T_{max} \approx \frac{3}{K} + t_o$. Note that T_{max} depends here only on the ratio $\frac{L_{max}}{L_\infty}$, on t_o and on K, not on size itself. (Note also that in very large, active, fishes such as tuna, billfishes and certain sharks the ratio $\frac{L_{max}}{L_\infty}$ is lower, say about 0.80 and that, therefore, $T_{max} \approx \frac{1.60}{K} + t_o$. The reasons for this will be presented elsewhere).

That there should be a relationship between K and M is, on the base of the relationship between K and T_{max}, quite evident, and attempts have been made relatively early to quantify this relationship such that it could be used to "set reasonable values of M in models, given K" (CUSHING, 1968).

BEVERTON & HOLT (1959) compiled data on growth parameters and M which can be used for such a purpose. These data have been adapted by CUSHING (1968, fig.50) who presented plots of M against K in Clupeiodei, Gadiforms, Salmonoidei and Pleuronectoidei which allow for rough estimates of M in these groups, given K. The CUSHING graphs and those of BEVERTON & HOLT (1959) have been widely used throughout the world and have certainly fulfilled the role assigned to them.

At present, however, these graphs are not sufficient. There is, first of all, a need to obtain estimates of M for various little investigated tropical or antarctic stocks which belong to none of the four taxa listed above. Furthermore, these estimates should be more precise than those obtained by plotting M on K. And finally, the question should be asked whether the apparent inter-taxa differences in the ratio M/K are due to intrinsic features of these taxa, or whether these differences are caused by the fact that other variables, such as size or environmental temperature, also have an influence on M/K.

CUSHING (1968) wrote that "the magnitude of M is probably the sum of predation for little fish; for predators it is more nearly a "physiological" mortality in a physiological sense, but is dependent on their place in the food chain". Similarly, URSIN (1967) stated that "natural mortality may have both physiological and environmental components. An example of the latter is the activity of predators".

Conceptually, we may split up mortality, in fact, into three components:

a) "Physiological" mortality, that is, mortality caused solely by disease, or old age, or both, and leading to death <u>without</u> the intervention of predators.

b) "Selective" mortality, that is, mortality caused by disease, or old age, or both, in a certain number of the fishes of a given stock, these fishes bing characterized by a lack of performance which first makes them accessible to predators.

c) "Chance" mortality, that is, mortality unrelated to any physiological mechanisms, and proportional only to the number of possible encounters with potential predators.

Physiological mortality, one should think, is proportional to K which, by its very nature (see equation 3) determines how long, at most, a fish is likely to live. Also, we may assume this purely physiological mortality to be the sole component of natural mortality only in very large fishes having (past their tender youth) no predators.

Selective mortality should represent as a whole, an important component of natural mortality mainly in middle-sized fishes. Selective mortality is well-known from terrestrial food chains (it is known, for example, that the proportion of sick, or otherwise disabled animals in a deer population tends to increase when the selective mortality exerted,say by wolves, is removed), but there are very few papers readily available documenting the existence of selective predation in marine or limnic food chains.

Finally, chance mortality is possibly the main component of natural mortality in small-sized fishes, which tend to be low in the food chain and have a large number of predators. Thus, "the situation is that small species have a higher natural mortality rate than big ones." (URSIN, 1967)

The relationship between size and mortality, however, is not a straightforward one. High values of M are generally correlated with small asymtotic size, but this is due primarily to the fact that low values of S are themselves correlated with high values of K. Thus, for example, it can be demonstrated that the plot of M against S in URSIN (1967), which yields a highly significant relationship, produces a non-significant relationship when the effect of the associated values of K is removed by partial correlation or multiple regression of logM against S and logK.(PAULY, MS)

The direct relationship between M and S indeed is so weak that it can be demonstrated only on the base of a large body of data, and after the effects of a third factor, environmental temperature, have been removed.

Preliminary suggestions as to why the mean environmental temperature should influence natural mortality will be presented in the Discussion.

This paper, thus, consists, in the main, of an attempt to demonstrate that at least three variables significantly and independently affect natural mortality:

1) the asymptotic size (L_∞ or W_∞),

2) the stress factor K, and

3) the environmental temperature.

This can be done, at once, by plotting values of logM against logS, logK and logT in a multiple linear regression of the form:

$$\log M = a + b\cdot\log S + c\cdot\log K + d\cdot\log T \qquad ....5)$$

and/or by testing the second-order partial correlation coefficients $r_{SM\cdot KT}$, $r_{KM\cdot ST}$ and $r_{TM\cdot KS}$. These correlation coefficients express the degree of association between, e.g., S and M, with the exclusion of the effect of K and T, and correspondingly for the other combinations of variables. (See e.g., SACHS 1974)

As the inductive basis gathered by earlier authors (e.g. BEVERTON & HOLT, 1959) seemed too small to test all these hypotheses, more data have been compiled whose origin and treatment are discussed below.

Material

A) Values of M, criteria for inclusion

The 122 values of M which form the core of this study were gathered in the frame of a rather thorough scanning of the literature on population dynamics and growth of fish (PAULY,1978). There are probably more values of M in the extant literature than these 122, but it may be quite safely assumed that the data listed here represent the majority of the values of M published to date. Thirty-seven (30%) of the values of M included come from the pioneering work of BEVERTON & HOLT (1959).

The rules for inclusion were as follows:

- when a range of values was given, their arithmetic mean was taken;
- when only the upper range was given, the value of M was not included;
- values of Z were considered equivalent to values of M only when the original authors had themselves assumed that $F = 0$, or $F \approx 0$;
- a value of M, further, was taken only if it could be reasonably assumed that M is more or less constant over the adult life span. Thus, for example, values for M relating to salmons or capelins were not included, as these fishes have life histories which end quite catastrophically; and
- values of M relating to odd-shaped fishes were not included (this applies here to a few values for rays and sea-horses only).

B) Growth parameters

The majority of the growth parameters presented in the literature are values of L_∞ and K_L. (The index "L" in K_L is here necessary in order to distinguish K_L from K_W, that is, from a value of K used in conjunction with W_∞. The values of K_L and K_W are equal, in a given stock, only when weight growth is isometric, that is, proportional to the third power of length). The values of L_∞ were converted to total length (LT) wherever other measurements had been made in all cases where the paper containing the original data was seen, that is, in the great majority of cases. It may be assumed that a few fork or even standard lengths were left among the data of Table I, but they should hardly bring any bias into the equations. Where W_∞ and K_W were not given by the original authors, conversions were made according to the following rules:

- Wherever a length-weight relationship of the form $W = a \cdot L^b$ was given that expressedly applied to the stock in question, this relationship was used to calculate, for each set of lengths-at-age, the corresponding set of weights-at-age, from which the values of W_∞ and K_W were determined. This technique was used wherever the values of K_L and K_W are not equal in Table I.
- Where a length-weight relationship for a given stock was not readily found, a good value for the condition factor (cf) was used to convert L_∞ to W_∞. ($cf = \frac{W \cdot 100}{L^3}$), with gutted weight in g and TL in cm)
  Such cases may be identified in Table I by the fact that $K_L = K_W$.
- In cases where a condition factor for the species in question could not be readily found, the condition factor of a closely related species (of similar shape) was taken. Estimates of W_∞ based on such conversions may be identified in Table I by the fact that they are enclosed in brackets.
- When two sets of growth parameters (e.g. for ♂♂ & ♀♀) faced one single value of M, the geometric means of the values of S and K were taken and included in Table I.

The methods used for the determination of values of S and K from the various sets of size-at-age data were the **FORD-WALFORD Plot** in all those cases where the data could not, or needed not be weighted by sample size, and non-linear regression for the data of HART (1931), where sample size had a serious effect on the parameter estimation.

The length-at-age data of SEMAKULA & LARKIN (1968), of SHINDO (1972) and of WEBER & JOTHY (1977) were processed by means of a "VON BERTALANFFY Plot", that is, by using set values of asymptotic size (See PAULY, 1978 for details).

C) Temperature

The temperature given for each stock in Table I is the mean annual temperature at the positions where the fish were caught (the "locations" given in Table I, as a whole, do not give all details referring to the actual positions. The letters with the locations stand for: M = Marine, F = Freshwater, D = Diadromous and B = Brackish.) These temperatures were estimated as follows:

For marine fishes:

- Pelagic and shallow water benthic fishes including brackish and diadromous: from the "Atlas of Sea Surface Temperatures" (ANON., 1944), by months, with subsequent averaging over the whole year and conversion from ^{o}F to ^{o}C.
- For deep benthic fishes (i.e. cods), the temperatures given are estimates of the mean annual temperature in the depth layer where the fish generally occur. These estimates were made by Dr. G. PRAHM of the Deutches Hydrographisches Institut, Hamburg, on the basis of position and depth data provided by this author.

For fresh water fishes:

- From the "Klimadiagram - Weltatlas" (WALTER & LIETH, 1967) on the assumption that the mean annual surface temperature, in fresh water bodies, roughly corresponds to the mean annual air temperature of the same area.

The temperature data were rounded to the next degree centigrade with the exception of stock No. 93 (See Discussion). It appears that below temperatures of about $+3^{o}$ C, any subsequent decrease of mean annual temperature has an effect upon the growth parameters similar to that caused, at higher temperatures, by an increase of temperature (namely a decrease of asymptotic size and an increase of the stress factor K, with corresponding effect on M). So, the linear regression model used here does not apply at very low temperatures if the real environmental temperature (T) is used. This "cold adaptation" effect, however, can be counteracted by using a value of T' instead of T at temperatures below $+3.5^{o}$ C. T' is then the higher temperature to which the scope of the "cold adapted" metabolism corresponds (See Discussion).

D) Statistical methods

1) Note that the common logarithm of all values of M, W_∞, L_∞, K_L, K_W and T was rounded off to 4 digits after the point, prior to all correlation and regression analysis.

2) Analysis of correlations

The relationship between variables have been investigated by means of two-variable correlation coefficients (r) and of multiple correlation coefficients (R). Two-variable correlation coefficients express the degree of association between two given variables irrespective of the potential effect of any other variables.

Multiple correlation coefficients, on the other hand, express the degree of association between a given variable and a set of other variables, without indicating which variable(s) correlate(s) best, and which do not correlate at all. So, in addition, it became necessary to calculate partial correlation coefficients, which express the degree of association between two variables after the effect of (an) additional variable(s) has been removed. First order partial correlation coefficients relating to three variables have the formula:

$$r_{12\cdot 3}=\frac{r_{12}-r_{13}\cdot r_{23}}{\sqrt{(1-r^2_{13})\cdot(1-r^2_{23})}} \qquad \ldots.6)$$

For the investigation of the interelationship between four variables, second order partial correlation coefficients are needed. They are calculated on the basis of first order partial correlation coefficients such that:

$$r_{12\cdot 34}=\frac{r_{12\cdot 4}-(r_{13\cdot 4}\cdot r_{23\cdot 4})}{\sqrt{(1-r^2_{13\cdot 4})\cdot(1-r^2_{23\cdot 4})}} \qquad \ldots.7)$$

where $r_{12\cdot 34}$ expresses the degree of association between variables 1 and 2 after the effects of variables 3 and 4 have been removed. (SACHS, 1974)

3) Regression analysis

Multiple linear regressions where calculated for two combinations of variables, namely $M = f(L_{\infty}, K_L, T)$ and $M = f(W_{\infty}, K_W, T)$ by means of Programme PP1, run in the Nova 1200 of the Department of Physical Oceanography, Institut für Meereskunde. The programme provides estimates of the multiple correlation coefficient, of the values of the different slopes and their standard deviations, as well as an estimate of the value of the standard deviation of the dependent variable.

Results

A) The mortality, growth and temperature data used for all subsequent computations are summarized in Table I (a to e).

B) The two variable correlation coefficients are given in Table II. All are highly significant, except that there is no correlation between temperature and asymptotic size.

C) The first order correlation coefficients are given in Table III. Note that there is no significant relationship between size and mortality when the effect of K alone is removed.

D) The second order partial correlation coefficients are given in Table IV. Note that $r_{MW \cdot TK}$ is highly significant. That is, there is a relationship between mortality and asymptotic weight, but it becomes apparent only after the effect of K and temperature have been removed.

E) The parameter values of two multiple regressions are given; equation 8) gives the parameter values of the regression of logM against $\log W_{\infty}$, logK and logT, while equation 9) gives the parameters for the regression of $\log L_{\infty}$, logK and logT. Both regressions are highly significant, the multiple correlation coefficients R being 0.800 and 0.817 respectively, while, with 118 degrees of freedom, a critical value of only 0.303 is necessary for significance at the 99% level of confidence (Table Va).

The standard deviations of the various slopes (partial regression coefficients) are also given (Table Vb) together with the corresponding coefficient of variation (c.v. = $\frac{sd}{\bar{x}}$). (Table Vc)

All slopes are significantly $\neq 0$ at 95% level of confidence. At the 99% level of confidence, all slopes are significant, except for the one relating $\log L_\infty$ to $\log M$. This feature is treated in the Discussion.

F) The means of the various parameter values are given in Table Vd. The "typical" fish hitherto investigated has the parameter values $L_\infty = 36.7$ cm LT, $K_L = 0.35$, $W_\infty = 628$ g , $K_W = 0.36$ and a mean condition factor of 1.00.

The value of $K_L < K_W$ indicates that this typical fish grows negatively allometrically, that is, when $W = a \cdot L^b$, then $b < 3$ (here 2.95).

Finally, this typical fish occurs at a mean annual water temperature of 12.4° C and has a value of $M = 0.547$.

Discussion

A) General

The results show beyond any reasonable doubt that natural mortality, in fishes, is related to K, to asymptotic size and to the mean environmental temperature of the stock's biotope. Also, it appears that the relationship between asymtotic size and mortality is so weak that it cannot be demonstrated unless the stronger effects of K and temperature are removed.

It will be noticed that W_∞ correlates more closely with M than L_∞ does. A possible interpretation may be that weight allows for better comparison between different stocks belonging to widely differing species despite the fact that the weight estimates are, in most cases, indirect estimates, based on conversions from length estimates. On the other hand, the effects of the length-to-weight conversion may negatively affect the fit of K_W values which measure the same process (deceleration of growth) as the original K_L estimates. As a whole, however, the equation using L_∞ and K_L has a better fit that the one using W_∞ and K_W because the slope of K is much higher than that of L_∞ or W_∞. When M is expressed as a function of W_∞, K_L and T, the value of $R = 0.816$ comes close to that of M as a function of L_∞, K_L and T ($R = 0.817$).

The standard deviation (s.d.) of estimates of logM (0.27) is quite high, but it could probably be considerably reduced by disconsidering the worst data of Table I (see Table VI for their identification). This procedure, however, seems premature at this point. The task set here was to convincingly demonstrate the existence and the character of the various interrelationships, rather than fiddle with the data in order to improve the various correlation coefficients.

At this stage, however, it is clear that some taxa differ markedly from the predicted values of M. The Clupeidae and Heterosomata are two taxa which have lower values of M than would be expected from the equations, while the estimated values for M are generally lower than the empirical values in Rastrelliger and Nemipterus spp. It would be premature, at this stage, to speculate on the character of these deviations. Further investigations will be conducted as to this point.

Fresh and brackish water fishes do not differ from the bulk of the (marine) fishes as far as their natural mortality is concerned.

B) The effect of temperature on natural mortality

Several hypotheses may be advanced to explain the surprisingly high partial correlation between the temperature estimates and the values of M. These hypotheses may be grouped into two sets:

I) There is no real correlation between M and temperature, but only between M and some unknown parameter which is itself correlated with temperature. Some "hidden" parameters could be:

   1) The "age" of a given ecosystem -tropical ecosystems have a longer history of undisturbed evolution, hence a higher number of intensive interspecific relationships, such as predation.(See PIANKA, 1970, KREBS, 1972 or DOBHZANSKY, 2950)

   2) The number of associated species and the complexity of the food web, both of which generally increase with mean environmental temperature. Note that 2) is closely related to 1).

3) Some other factor correlated with temperature (See e.g., NURSALL, 1977, who plotted the intensity of biotic interactions against latitude).

II) There is a real direct correlation between M and environmental temperature. The cause for such a relationship could be:

1) Temperature, which determines M via K and via the asymptotic size, may also affect M directly by increasing "physiological" mortality (as defined in the Introduction).
2) Fishes occurring at higher temperatures have more chances to have encounters with "hungry" predators (rather than with satiated ones) because, other things being equal, tropical fishes have to eat more than the temperate fishes in order to satisfy their higher metabolic needs (WINBERG, 1960). This should force predatory fishes to eat more prey fishes per unit time than their cold-water counterparts, which would then result in higher natural mortality in the prey fishes.

Hypotheses I_1 and II_2 seem, at this point, to be the most likely.

C) Cold adaptations

WOHLSCHLAG (1960) discovered in respiration experiments that the antarctic fish Trematomus bernachii displays a rate of metabolism much higher than what would be expected by a simple extrapolation, down to antarctic temperatures, of KROGH'S "standard curve" of metabolism against temperature (See WINBERG, 1960 or 1971). This effect, previously reported by SCHOLANDER et al.(1957) and termed "cold adaptation", seems to apply to al fishes of very cold waters ($< + 3.5^{\circ}$ C). Cold adaptation also is the cause for the marked reduction of L_{∞} (or W_{∞}) and for the increase of K reported by students of some arctic fishes (See MAY et al., 1956 or SUVOROV, 1956) and for which a proper explanation is still wanting.

Pending a detailed discussion of this phenomenon (PAULY, in prep.) a table has been prepared (Table VII) whose values of T' should be used in conjunction with equation 8 or 9 for temperatures below + 3.5°C and which should largely offset the effects of cold adaptation on estimates of M in arctic and antarctic fishes. Table VII has been derived graphically from the compilation of metabolic rates in WOHLSCHLAG (1964) and from a few preliminary plots of L_∞ and K against temperature in various polar fishes. The data and details will be given elsewhere (PAULY, in prep.).

[Note than an arbitrary value of +1°C was used here for the Notothenia neglecta stock (No. 93 in Table I) instead of a value of T' derived from the mean environmental temperature (-0.85°C) reported by EVERSON (1970). Note also that this resulted in a particularly bad estimate of M (Table VI). The use of T' = 11.2°C, on the other hand, produces, with equation 9, an estimate of M = 0.21, against 0.36 for the empirical value, the difference being well within one standard deviation.]

D) The use of the reported relationships in population dynamics of fish

Considering the degree of uncertainty or even of arbitrariness which is characteristic of very many estimates of M, it would seem that the values of M provided by equation 8 or 9 are as good as most values presently in use for fishery management purposes. Indeed, it will hardly ever be possible to obtain independent estimates of M for the hundreds of species which, for example, form the base of the demersal fisheries of South East Asia (See MARR, 1976).

Equations 8 and 9, on the other hand, provide reasonable, estimates for M in any species of fish. Thus, for example, M can be estimated for Leiognathus splendens, an important species in the Sunda Shelf Area, by inserting the following parameters into equation 9: L_∞ = 14.3, K = 1.04 (PAULY, 1978) and T = 28.5°C (MARTOSUBROTO & PAULY, 1976). This provides an estimate of M = 1.83, which is quite close to the speculative value of M = 2.0 used in previous stock estimates (PAULY, 1977).

So, it appears that fishery biologists will now be able to make yield assessments in the field, using growth parameters compilations (such as PAULY, 1978), the Yield Tables of BEVERTON & HOLT (1966) and... a thermometer.

E) Addendum: Estimation of Catchability Coefficient (q)

The method commonly used to date to obtain estimates of M in exploited populations has been to plot values of total mortality (Z) against their corresponding values of effort (f), over a series of years where effort has been changing. The plot has the form:

$$y = a + bx \qquad ....10)$$

where y = Z, a = M, x = f and b = q, the catchability coefficient. Where no values of Z and f over a number of years are available, q has to be estimated from:

1) tagging experiments, generally rather expensive and often a sheer impossibility as, for example, in certain tropical stocks where the tagged fish simply disappear;

or, in demersal stocks by

2) the "swept area" method, which is fraught with uncertainties, especially concerning the number of fishes caught that are in the path of the trawl.

An additional use of equation 8 and equation 9, as presented above, is given by the fact that they produce values of M which can be used to estimate values of q , given a single value of Z with its corresponding value of effort. Say, for example, we know that in 1978 the trawler fleet of country A consists of 520 units (similar boats, all operating similarly) totalling 520 x 220 fishing days per year = 114 400 fishing days in that year. Say, also, that the mean value of Z for the stock in question was, in 1978, 0.80. Say, finally, that we know the growth parameter of this stock, and that they produce, when combined with the mean annual temperature at the fishing grounds, a value of M = 0.35. Then, F = 0.80 - 0.35. With F = 0.45, it follows that $q = \frac{0.45}{114\ 400} = 0.000004$.

This method for estimating q is not new. RICKER (1975) discussed its application to the Arcto-Norwegian Cod (pp. 172-174). The point here is that it can now be used as a routine method, since it is now easier to estimate M than it is to estimate q .

Table Ia. Raw data on growth, temperature and mortality

Nr.	Species	Family	Location	T °C	L_∞	K	W_∞	K	Author(s)	M	Author(s), if diff
1	Lamna nasus	Lamnidae	North East Atlantic, M	7	280.	0.111	166800.	0.111	Aasen (1963)	0.18	-
2	Acipenser fulvescens	Acipenseridae	Wisconsin, USA, F	8	178.	0.05	(36000.)	0.05	B & H (1959)	0.01	-
3	Acipenser transmontanus	"	Canada, Fraser River, D	10	350.	0.040	96680.	0.038	Semakula & Larkin (1968)	0.05	-
4	A. transmontanus/ A. medirostris	"	Gulf of California, D	22	300.	0.06	170000.	0.06	Pycha (1956)	0.03	B & H (1959)
5	Clupea harengus	Clupeidae	North Sea, M	11	30.	0.38	200.	0.38	B & H (1959)	0.25	-
6	" "	"	Atlanto-Scandian Stock, M	8	36.	0.21	350.	0.21	B & H (1959)	0.16	-
7	" "	"	Northern Baltic, B	8	19.4	0.4	55.	0.4	Thurow (1976)	0.35	-
8	" "	"	Southern Baltic, B	9	27.7	0.48	160.	0.48	Thurow (1976)	0.36	-
9	" "	"	Irish Sea, M	12	29.5	0.39	193.	0.39	Beverton (1963)	0.20	-
10	" pallasii	"	Hokkaido, Japan, M	12	38.5	0.19	525.	0.207	Beverton (1963)	0.2	-
11	" "	"	British Columbia, Can. M	10	27.	0.48	209.	0.492	Beverton (1963)	0.5	-
12	Sardinella longiceps	"	Southern India, M	27	20.7	0.528	62.6	0.542	Banerjii (1973)	0.67	-
13	Sardinops caerula	"	California, M	15	29.3	0.45	337.	0.454	Beverton (1963)	0.40	-
14	" "	"	"	15	30.	0.350	225.	0.383	Marr (1960)	0.45	Clark & Marr (1955)
15	" melanostica	"	Japan, M	15	27.	0.9	209.	0.902	Holt (1960)	0.5	-
16	Sprattus sprattus	"	Western Baltic, B	9	14.4	0.298	20.4	0.27	Rechlin (1974)	0.7	Thurow (1976)
17	Engraulis encrasicholus	Engraulidae	European Waters, M	15	14.9	1.13	24.	1.123	Bayliff (1967)	1.80	-
18	" japonicus	"	Japan, M	20	17.7	1.8	(36.)	1.80	Bayliff (1967)	1.63	-
19	" anchoita	"	Argentina, M	16	23.2	0.27	212.	0.23	Bayliff (1967)	1.42	-
20	" "	"	"	16	17.3	0.713	50.	0.713	Brandhorst et al. (1974)	0.9	-
21	" ringens	"	Peru, M	16	17.	1.40	37.	1.389	Bayliff (1967)	1.0	-
22	" "	"	Peru, M	16	15.	1.7	24.	1.688	Boerema et al (1965)	1.52	-
23	" mordax	"	California, M	15	16.4	0.45	21.	0.45	Bayliff (1967)	1.70	-
24	Cetengraulis mysticetus	"	Central America, (W.),M	24	18.	1.99	56.	2.032	Bayliff (1967)	2.40	-

Table Ib. Raw data on growth, temperature and mortality.

Nr.	Species	Family	Location	T °C	L_∞	K	W_∞	K	Author(s)	M	Author(s) if diff.
25	Salmo trutta	Salmonidae	England, Lake Distr., F	9	30.	0.36	300.	0.36	B & H (1959)	0.94	
26	Coregonus clupeaformis	"	Shakesp. Isl.Lake, Can. F	3	58.3	0.088	2826.	0.079	Hart (1931)	0.15	B & H (1959)
27	" "	"	Lake Nipigon, Can., F	3	70.	0.082	6215.	0.063	Hart (1931)	0.17	B & H (1959)
28	" "	"	L. Opeongo, Can., F	3	14.	0.43	27.	0.43	B & H (1959)	0.9	-
29	Leucichthys artedi	"	Wisconsin, Trout.Lake, F	8	19.	0.65	(70.)	0.65	B & H (1959)	1.1	-
30	" "	"	", Musk llunge L., F	8	21.	0.36	(95.)	0.36	B & H (1959)	1.2	-
31	" "	"	", Clear L., F	8	39.	0.27	(600.)	0.27	B & H (1959)	0.35	-
32	" sardinella	"	Alaska/Tasmania, F	3	38.	0.40	(550.)	0.4	B & H (1959)	0.6	-
33	Esox lucius ♂	Esocidae	Windermere L., Engl., F	9	75.	0.24	3288.	0.24	Johnson (1966)	0.24	-
34	" " ♀	"	" " F	9	100.	0.22	8810.	0.22	Johnson (1966)	0.26	-
35	Saurida tumbil	Synodontidae	East China Sea, M	17	69.5	0.286	2350.	0.286	Shindo (1972)	0.46	Pauly, data of Shindo (1972)
36	Benthosema glaciale	Myctophidae	North West Atlantic, M	7	8.5	0.36	(5.6)	0.36	Gjösaeter (1973)	1.75	"
37	" "	"	Norwegian Fjords, M	7	8.6	0.45	(5.7)	0.45	Gjösaeter (1973)	0.74	"
38	Phoxinus phoxinus	Cyprinidae	Windermere L., Engl. F	9	9.1	0.58	8.2	0.58	Frost (1943)	1.1	B & H (1959)
39	Trisopterus esmarkii	Gadidae	off Scotland, M	9	19.3	0.59	48.	0.59	Raitt (1968)	1.6	-
40	" "	"	" " M	9	19.0	0.44	45.	0.44	Raitt (1968)	1.6	-
41	Gadus minutus ♂	"	English Channel, M	12	16.8	1.372	59.4	1.372	Menon (1950)	1.1	B & H (1959)
42	" " ♀	"	" "	12	26.3	0.465	158.	0.465	Menon (1950)	0.9	B & H (1959)
43	Melanogrammus aeglefinus	"	New England, M	5	73.	0.28	2150.	0.297	Beverton (1965)	0.20	Taylor (1958)
44	Pollachius virens	"	Iceland, M	3	128.	0.13	20077.	0.13	Jones & Jonsson (1971)	0.3	-
45	" "	"	Norwegian Sea, M	6	107	0.19	11634.	0.19	B & H (1957)	0.15	-
46	" "	"	Iceland, M	3	120.	0.15	16514.	0.15	Jones & Jonsson (1971)	0.3	-
47	Gadus morhua	"	Faroe Plateau, M	8	115.	0.19	16350.	0.181	Jones (1966)	0.17	-
48	" "	"	Grand Bank, M	2	116.	0.114	11720.	0.123	Clayden (1972)	0.20	-

Table Ic. Raw data on growth, temperature and mortality.

Nr.	Species	Family	Location	T °C	L_∞	K	W_∞	K	Author(s)	M	Author(s), if diff.
49	Gadus morhua	Gadidae	ICNAF 2J, M	1	67.	0.28	3000.	0.28	May *et al.* (1965) & Figueras (1964)	0.18	Pinhorn (1975)
50	" "	"	North Sea, M	8	132.	0.20	20000.	0.20	B & H (1957)	0.2	B & H (1959)
51	" "	"	Gdansk Deep, Baltic, B	5	112.	0.154	10834.	0.166	Kändler (1944)	0.31	Thurow (1971)
52	" "	"	Bornholm, Baltic, B	6	100.	0.2	8158.	0.211	Kändler (1944)	0.44	Thurow (1971)
53	Merluccius merluccius ♂	Merluccidae	Marmara Sea, M	15	44.	0.13	622.	0.13	B & H (1959)	0.6	-
54	" " ♀	"	" " M	15	60.	0.10	1577.	0.10	B & H (1959)	0.5	-
55	" productus	"	US, West Coast, M	12	61.	0.30	1272.	0.324	Dark (1975)	0.56	Ehrich, pers. comm.
56	" angustimanus	"	Gulf of California, M	20	32.7	0.35	(255.)	0.35	Matthew (1975)	0.84	-
57	Cololabis saira	Scomberesocidae	US, West Coast, M	12	36.6	0.42	189.	0.42	Hughes (1974)	1.60	-
58	Gasterosteus aculeatus	Gasterosteidae	Cheshire, England, F	10	6.7	0.64	1.8	0.64	B & H (1959)	0.9	-
59	Pungitius pungitius	"	" " , F	10	4.3	1.6	(0.4)	1.6	B & H (1959)	1.1	-
60	Cottus gobio ♂	Cottidae	River Brathey, Engl.,F	9	6.5	0.9	4.3	0.9	B & H (1959)	1.1	-
61	" " ♀	"	" " " ,F	9	6.5	0.4	4.3	0.4	B & H (1959)	0.8	-
62	" " ♂	"	Windermere L. Engl., F	9	7.2	0.7	5.9	0.7	B & H (1959)	1.1	-
63	" " ♀	"	" " , F	9	7.3	0.4	6.1	0.4	B& H (1959)	0.9	-
64	Dicentrachus labrax	Serranidae	Southern Ireland, M	10	71.4	0.14	6860.	0.13	Holden & William (1974)	0.10	-
65	Epinephelus guttatus	"	Reefs, Jamaica, M	27	52.	0.24	2090.	0.243	Thompson & Munro (1977)	0.68	-
66	" striatus	"	" " , M	27	90.	0.09	16000.	0.09	Thompson & Munro (1977)	0.24	-
67	Cephalopholis fulva	"	" " , M	27	34.	0.63	633.	0.658	Thompson & Munro (1977)	0.55	-
68	Mycteroperca venenosa	"	" " , M	27	86.	0.18	(8330.)	0.18	Thompson & Munro (1977)	0.42	-
69	Perca fluviatilis	Percidae	Sweden, ponds, F	6	30.	0.20	435.	0.20	B & H (1959)	0.29	-
70	" "	"	Sweden, ponds, F	6	34.	0.13	633.	0.13	B & H (1959)	0.16	-
71	Stizostedion canadensis	"	Lake Nipigon, Can., F	3	40.	0.13	(615.)	0.13	B & H (1959)	0.44	-
72	Trachurus japonicus	Carangidae	Sea of Japan, M	20	51.2	0.28	1188.	0.28	Kim *et al.* (1969)	0.99	Mitani & Shojima (1966)

Table Id. Raw data on growth, temperature and mortality.

Nr.	Species	Family	Location	T °C	L_∞	K	W_∞	K	Author(s)		Author(s) if diff.
73	Lutjanus purpureus	Lutjanidae	Northern Brazil, M	27	96.7	0.096	11664.	0.096	Fonteles-Filho (1970)	0.37	Ivo & Gesteira
74	Nemipterus bleekeri	Nemipteridae	" Borneo, M	28	31.	0.437	(300.)	0.437	Weber & Jothy (1977)	1.41	- (1974)
75	" delagoae	"	" " , M	28	28.9	0.703	(240.)	0.703	" "	2.19	
76	" hexodon	"	" " , M	28	27.8	0.511	(215.)	0.511	" "	0.95	-
77	" japonicus	"	" " , M	28	29.5	0.458	(255.)	0.458	" "	2.28	-
78	" marginatus	"	" " , M	28	28.4	0.363	(230.)	0.363	" "	1.56	-
79	" nematophorus	"	" " , M	28	27.3	0.986	(200.)	0.986	" "	1.89	-
80	" mesoprion	"	" " , M	28	19.5	0.626	(75.)	0.626	" "	0.62	-
81	" nemurus	"	" " , M	28	29.0	0.276	(245.)	0.276	" "	1.31	-
82	" peronii	"	" " , M	28	29.5	0.500	(257.)	0.500	" "	1.41	-
83	" tolu	"	" " , M	28	28.5	0.437	(230.)	0.437	" "	0.41	-
84	Lethrinus enigmaticus	Lethrinidae	Indian Ocean, M	27	53.5	0.163	2916.	0.154	Lebeau & Cueff (1975)	0.2	-
85	Cynoscion macdonaldi	Sciaenidae	Venezuela, M	27	128.	0.3	17826.	0.3	B & H (1959)	0.3	-
86	" nobilis	"	Florida, M	24	146.	0.128	27900.	0.132	Thomas (1968)	0.3	-
87	Pseudosciaena diacanthus	"	Bombay, India, M	27	122.	0.315	17400.	0.32	Rao (1966)	0.8	Rao (1968)
88	Pseudotolithus elongatus	"	Congo River Estuary, M	26	46.7	0.274	715.	0.274	Le Gueu (1971)	0.34	
89	Mulloidichthys martinicus	Mullidae	Reefs, Jamaica, M	27	34.2	0.4	429.	0.41	Munro (1976)	1.7	-
90	Pseudoupeneus maculatus	"	" " , M	27	31.2	0.7	390.	0.687	Munro (1976)	1.89	-
91	Cheilodactylus macropterus	Cheilodactylidae	New Zealand, M	14	47.7	0.279	1390.	0.283	Vooren (1977)	0.08	-
92	Mugil cephalus ♂	Mugilidae	Taiwan, M	20	49.8	0.393	2450.	0.393	Ih-Hsiu Tung (1970)	0.31	-
93	Notothenia neglecta	Notothenidae	Antarctica, M	(+1)	48.4	0.108	2178.	0.108	Everson (1970)	0.36	-
94	Blennius pholis	Blennidae	English Channel, M	12	17.	0.3	54.	0.3	B & H (1959)	0.9	-
95	Ammodytes marinus	Ammodytidae	North Sea, M	11	21.8	0.89	32.1	0.89	Reay (1972)	1.24	Reay (1973)
96	" tobianus	"	" " , M	11	16.6	0.77	15.0	0.778	Reay (1973)	1.29	
97	Callionymus lyra ♂	Callionymidae	English Channel, M	12	25.	0.43	7.8	0.43	B & H (1959)	0.96	-
98	" " ♀	"	" " , M	12	17.5	0.55	(27.)	0.55	B & H (1959)	0.86	-

Table Ie. Raw data on growth, temperature and mortality.

Nr.	Species	Family	Location	T °C	L_∞	K	W_∞	K	Author(s)	M	Author(s) if diff.
99	Pneumatophorus japonicus	Scombridae	California, M	15	40.	0.4	810.	0.38	B & H (1959)	0.9	-
100	Rastrelliger kanagurta	"	Java Sea, M	28	23.9	2.76	160.	2.60	Sudjastani (1973)	4.44	-
101	" "	"	India, M	27	23.9	4.92	154.	4.786	Banerji (1973)	7.80	-
102	" neglectus	"	Gulf of Thailand, M	28	20.9	3.38	110.	3.212	Hongskul (1974)	7.22	-
103	" "	"	" " , M	28	20.9	4.2	84.	4.126	Somjaiwong *et al.* (1972)	4.2	-
104	" "	"	Western Borneo, M	28	22.9	2.28	205.	2.385	Sudjastani (1973)	4.56	-
105	Katsuwonus pelamis	Thunnidae	Eastern Pacific, M	25	113.	0.42	32300.	0.42	Joseph & Calkins (1969)	1.68	-
106	Thunnus alalunga	"	Central Atlantic, M	25	151.	0.141	58760.	0.141	Beardsley 1971	0.23	-
107	" "	"	Eastern " , M	26	143.	0.183	5150.	0.183	in: Le Gall (1974)	0.20	Bard (1973)
108	" albacares	"	Hawaii, M	25	205.	0.454	144400.	0.427	Moore (1951)	0.8	B & H (1959)
109	" "	"	Central East Pacific, M	25	244.	0.240	199000.	0.250	Wise (1972)	0.9	-
110	" "	"	" " " , M	25	182.	0.63	98970.	0.63	Hennemuth (1961a)	0.77	Hennemuth (1961b)
111	" "	"	Eastern Atlantic, M	26	210.	0.42	137500.	0.422	Le Gueu & Sagakawa ('73)	0.8	-
112	" atlanticus	"	West Atlantic, M	26	83.	0.33	9760.	0.328	Carles Martin (1975)	0.67	-
113	" germo	"	Pacific, M	25	144.	0.172	36900.	0.203	Clemens (1961)	0.22	Tauchi (1940)
114	" maccoyi	"	Australia, M	26	235.	0.151	195660.	0.157	Hynd & Lucas (1974)	0.2	-
115	Eopsetta jordani ♂	Pleuronectidae	Canada, West Coast, M	9	49.	0.160	4566.	0.148	Ketchen & Forrester ('66)	0.25	-
116	" " ♀	"	" " , M	9	58.6	0.167	3970.	0.135	" " (1966)	0.20	-
117	Platychthys flesus	"	Kiel Bay, Baltic, B	8	42.6	0.869	1040.	0.869	Saeger (1974)	0.18	-
118	Pseudopleuronectes americanus	"	Canada, East Coast, M	5	44.	0.4	1380.	0.371	B & H (1959)	0.4	-
119	Pleuronectes platessa ♂	"	North Sea, M	7	45.	0.15	910.	0.15	B & H (1959)	0.22	-
120	" " ♀	"	" " , M	7	70.	0.08	3430.	0.08	"	0.12	-
121	Solea vulgaris	Soleidae	" " , M	7	37.7	0.42	482.	0.42	"	0.25	-
122	Cynoglossus macrolepidus	Cynoglossidae	Cochin, India, M	27	31.6	0.239	170.	0.204	Krishan Kutty & Qasim (1969)	0.49	-

Table II. Two-variable correlation coefficients.

	W_∞	L_∞	K_W	K_L	T	M
W_∞	-	0.981	-0.548	-0.622	0.029^{+}	-0.555
L_∞	0.981	-	-0.548	-0.626	0.014^{+}	-0.564
K_W	-0.548	-0.548	-	0.917	0.258	-0.742
K_L	-0.622	-0.626	0.917	-	0.338	0.799
T	0.029^{+}	0.014^{+}	0.258	0.338	-	0.381
M	-0.555	-0.564	0.742	0.799	0.381	-

Critical values: 0.248 (99%) and 0.178 (95%). DF = 120 (n - 2). Dash: self-correlation. $^{+}$Not significant at 95%.

Table III. First order partial correlation coefficients.

	M, W, K_W, T		M, L, K_L, T
$r_{MK\cdot W}$	0.629	$r_{MK\cdot L}$	0.629
$r_{MK\cdot T}$	0.721	$r_{MK\cdot T}$	0.770
$r_{KT\cdot M}$	-0.040^{+}	$r_{KT\cdot M}$	0.060^{+}
$r_{KT\cdot W}$	0.328	$r_{KT\cdot L}$	0.445
$r_{MT\cdot K}$	0.293	$r_{MT\cdot K}$	0.196^{+}
$r_{MT\cdot W}$	0.478	$r_{MT\cdot L}$	0.471
$r_{WM\cdot K}$	-0.265^{+}	$r_{LM\cdot K}$	-0.136^{+}
$r_{WM\cdot T}$	-0.612	$r_{LM\cdot T}$	-0.616
$r_{WT\cdot M}$	0.307	$r_{LT\cdot M}$	0.300
$r_{WT\cdot K}$	0.211^{+}	$r_{LT\cdot K}$	0.307

Critical values: 0.273 (99%) and 0.235 (95%). DF = 119 (n - 3). $^{+}$Not significant at 95% level.

Table IV. Second order partial correlation coefficients

$r_{MK \cdot TW}$	0.569	$r_{MK \cdot TL}$	0.611
$r_{MT \cdot KW}$	0.370	$r_{MT \cdot KL}$	0.252^{+}
$r_{MW \cdot TK}$	-0.350	$r_{ML \cdot TK}$	-0.210^{+}

Critical values: 0.303 (99%) and 0.254 (95%). DF = 118 (n - 4).
$^{+}$Not significant at 95% level.

Table V. Basic equations. Summary of data.

a)

Equation	M=	a	b	c	d	R
No. 8	$f(W_{\infty}, K_W, T)$	-0.1091	-0.1017	+0.5912	+0.3598	0.800
No. 9	$f(L_{\infty}, K_L, T)$	+0.1228	-0.1912	+0.7485	+0.2391	0.817

Critical value: R = 0.303(99%). DF = 118

b)

Standard deviation	of b	of c	of d	for estimates of M
Equation No. 8	0.0251	0.0783	0.0831	0.27655
Equation No. 9	0.0812	0.0893	0.0842	0.26559

c)

Coefficients of variation	of b	of c	of d
Equation No. 8	24.7%	13.2%	23.1%
Equation No. 9	42.5%	11.9%	35.2%

d)

	$\log L_{\infty}$	$\log K_L$	$\log W_{\infty}$	$\log K_W$	$\log T$	$\log M$
mean	1.5989	-0.4553	2.7992	-0.4431	1.0941	-0.2621
std. deviation	0.4003	0.3869	1.2231	0.4058	0.3201	0.4549

	L_{∞}	K_L	W_{∞}	K_W	T	M
geometric mean	39.7	0.350	628.	0.360	12.4	0.547

mean condition factor (for $\overline{L}_{\infty}$ & $\overline{W}_{\infty}$) = 1.00

Table VIa. Estimated values of $\hat{M}$ based on equation 9, ranked according to the deviation from M.

No.	Species	M	$\hat{M}$	% deviation -	 +	
2	Acipenser fulvescens	0.01	0.09	88.4	-	M < M - s.d.
91	Cheilodactylus macropterus	0.08	0.46	82.5	-	
117	Platychthys flesus	0.18	0.96	81.2	-	
4	Acipenser spp.	0.03	0.11	73.6	-	
9	Clupea harengus	0.20	0.62	67.8	-	
15	Sardinops melanostica	0.5	1.25	59.9	-	
5	Clupea harengus	0.25	0.60	58.0	-	
64	Dicentrachus labrax	0.10	0.23	57.2	-	
59	Pungitius pungitius	1.1	2.47	55.6	-	
121	Solea vulgaris	0.25	0.55	54.7	-	
6	Clupea harengus	0.16	0.34	53.2	-	
92	Mugil cephalus ♂	0.31	0.64	51.5	-	
83	Nemipterus tolu	0.41	0.83	50.9	-	
7	Clupea harengus	0.35	0.62	48.8	-	
88	Pseudotolithus elongatus	0.34	0.66	48.2	-	
21	Engraulis ringens	1.00	1.93	48.1	-	
67	Cephalopholis fulva	0.55	1.05	47.7	-	
8	Clupea harengus	0.36	0.69	47.5	-	
80	Nemipterus mesoprion	0.62	1.17	47.2	-	
13	Sardinops caerula	0.40	0.73	45.3	-	
84	Lethrinus enigmaticus	0.2	0.35	43.0	-	
10	Clupea pallasii	0.2	0.35	42.0	-	
43	Melanogrammus aeglefinus	0.2	0.33	39.6	-	
41	Gadus minutus ♂	1.1	1.78	38.1	-	
60	Cottus gobio ♂	0.9	1.45	37.9		
85	Cynoscion macdonaldi	0.3	0.47	36.0	-	
45	Pollachius virens	0.15	0.24	37.6	-	
107	Thunnus alalunga	0.20	0.31	36.3	-	
12	Sardinella longiceps	0.67	1.01	33.9	-	
22	Engraulis ringens	1.52	2.28	33.4	-	
47	Gadus morhua	0.17	0.25	33.1	-	
18	Engraulis japonicus	1.63	2.43	33.0	-	
11	Clupea pallasii	0.5	0.71	29.3	-	
70	Perca fluviatilis	0.16	0.23	29.0	-	
33	Esox lucius ♂	0.24	0.34	28.9	-	
116	Eopsetta jordani ♀	0.20	0.27	25.9	-	
113	Thunnus germo	0.22	0.30	25.8	-	
3	Acipenser transmontanus	0.05	0.07	25.6	-	
14	Sardinops caerula	0.45	0.60	25.4	-	
20	Engraulis anchoita	0.9	1.16	22.3	-	
50	Gadus morhua	0.2	0.26	22.2	-	
49	Gadus morhua	0.18	0.23	21.4	-	
58	Gasterosteus aculeatus	0.9	1.15	21.4	-	
114	Thunnus maccoyi	0.2	0.25	19.1	-	
118	P. americanus	0.4	0.48	16.0	-	
120	Pleuronectes platessa ♀	0.12	0.14	15.2	-	
31	Leucichthys artedi	0.35	0.41	13.9	-	
34	Esox lucius ♀	0.26	0.30	13.2	-	
103	Rastrelliger neglectus	4.2	4.82	12.8	-	
24	Centengraulis mysticetus	2.40	2.73	12.2	-	
119	Pleuronectes platessa ♂	0.22	0.25	10.8	-	
106	Thunnus alalunga	0.23	0.25	9.2	-	
69	Perca fluviatilis	0.29	0.32	9.0	-	
115	Eopsetta jordani ♂	0.25	0.27	7.6	-	
62	Cottus gobio ♂	1.1	1.18	6.6	-	
122	Cynoglossus macrolepidus	0.49	0.52	5.1	-	
37	Benthosema glaciale	0.74	0.77	3.9	-	
98	Callionymus lyra ♀	0.86	0.89	3.3	-	
76	Nemipterus hexodon	0.95	0.94	-	.8	
35	Saurida tumbil	0.46	0.45	-	1.13	
61	Cottus gobio ♀	0.8	0.79	-	1.25	
110	Thunnus albacares	0.77	0.75	-	2.8	

Table VIb. Estimated values of $\hat{M}$ based on equation 9, ranked according to the deviation from M.

No.	Species	M	$\hat{M}$	% deviation -	+
95	Ammodytes marinus	1.24	1.20	-	3.6
17	Engraulis encrasicholus	1.80	1.66	-	8.6
38	Phoxinus phoxinus	1.1	0.98	-	12.4
96	Ammodytes tobianus	1.29	1.13	-	14.0
63	Cottus gobio ♀	0.9	0.77	-	16.5
26	Coregonus clupeaformis	0.15	0.13	-	16.7
66	Epinephelus striatus	0.24	0.20	-	17.9
68	Mycteroperca venenosa	0.42	0.34	-	21.8
79	Nemipterus nematophorus	1.89	1.55	-	22.1
29	Leucichthys artedi	1.1	0.90	-	22.2
112	Thunnus atlanticus	0.67	0.54	-	23.7
55	Merluccius productus	0.56	0.44	-	25.9
42	Gadus minutus ♀	0.9	0.73	-	24.1
86	Cynoscion nobilis	0.3	0.23	-	27.8
16	Sprattus sprattus	0.7	0.54	-	28.6
100	Rastrellinger kanagurta	4.44	3.43	-	29.5
1	Lamna nasus	0.18	0.14	-	29.7
56	Merluccius angustimanus	0.84	0.64	-	32.2
32	Leucichthys sardinella	0.6	0.43	-	38.4
97	Callionymus lyra ♂	0.96	0.69	-	39.0
108	Thunnus albacares	0.8	0.57	-	39.6
65	Epinephelus guttatus	0.68	0.47	-	44.4
27	Coregonus clupeaformis	0.17	0.12	-	44.4
111	Thunnus albacares	0.8	0.54	-	47.2
99	Pneumatophorus japonicus	0.9	0.63	-	47.7
101	Rastrelliger kanagurta	7.80	5.24	-	48.8
104	Rastrelliger neglectus	4.56	3.00	-	52.1
82	Nemipterus peronii	1.41	0.92	-	53.7
94	Blennius pholis	0.9	0.57	-	58.5
51	Gadus morhua	0.31	0.15	-	59.0
48	Gadus morhua	0.2	0.12	-	61.0
28	Coregonus clupeaformis	0.9	0.55	-	62.5
87	Pseudosciaena diacanthus	0.8	0.49	-	63.1
90	Pseudoupeneus maculatus	1.89	1.16	-	63.3
74	Nemipterus bleekeri	1.41	0.82	-	71.7
25	Salmo trutta	0.94	0.55	-	72.5
52	Gadus morhua	0.44	0.25	-	73.9
73	Lutjanus purpureus	0.37	0.21	-	75.6
102	Rastrelliger neglectus	7.22	4.10	-	76.3
75	Nemipterus delagoae	2.19	1.19	-	84.3
39	Trisopterus esmarkii	1.6	0.86	-	86.4
72	Trachurus japonicus	0.99	0.49	-	100.6
44	Pollachius virens	0.3	0.15	-	102.5
23	Engraulis mordax	1.70	0.82	-	108.1
30	Leucichthys artedi	1.2	0.57	-	111.5
46	Pollachius virens	0.3	0.17	-	114.1
78	Nemipterus marginatus	1.56	0.73	-	114.6
81	Nemipterus nemurus	1.31	0.59	-	122.1
53	Merluccius merluccius ♂	0.6	0.27	-	124.7
89	Mulloidichthys martinicus	1.7	0.75	-	127.3
40	Trisopterus esmarkii	1.6	0.69	-	131.5
71	Stizostedion canadensis	0.44	0.19	-	137.8
54	Merluccius merluccius ♀	0.5	0.21	-	141.8
57	Cololabis saira	1.60	0.63	-	153.7
109	Thunnus albacares	0.9	0.34	-	161.6
77	Nemipterus japonicus	2.28	0.86	-	165.5
36	Benthosema glaciale	1.75	0.65	-	167.9
19	Engraulis anchoita	1.42	0.53	-	168.1
105	Katsuwonus pelamis	1.68	0.61	-	177.3
93	Notothenia neglecta	0.36	0.12	-	201.4

↓ $M > \hat{M} + s.d.$

Table VII. Table of conversion for temperatures below +3.5° C[§]

instead of T=	use T'=	instead of T=	use T'=
-2.0	+12.8	+0.5	+6.7
-1.5	+11.6	+1.0	+5.9
-1.0	+10.3	+1.5	+5.3
-0.5	+ 8.9	+2.0	+5.0
0.0	+ 7.7	+2.5	+4.6
		+3.0	+4.2

[§] from 3.5° C and up: T = T'. Find intermediate values through linear interpolation.

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NOTE:

Pending the publication of a revised and expanded version of the present paper, a limited number of copies have been reprinted for private distribution. This opportunity is taken to provide a short corrigendum:

1) In Stock No. 63, a value of M = 1.1 was used for the calculation instead of the correct value of M = 0.9.

2) In Stock No. 116, the value of K_L and K_W should read 0.34 instead of 0.869. This stock consequently has a value of M much closer to the predicted value than suggested in Table VIa.

3) As a consequence of 1) and 2), the correlation coefficients of the equations should improve slightly, and the standard deviation of M estimates should be somewhat smaller.

4) The reference to the most important paper cited in this investigation was omitted. It is:

   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 Foundation Colloquia on Ageing 5: 142 - 180.

5) Change of author's address effective 1 July 1979:

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