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# ESTIMATION OF NATURAL MORTALITY IN FISH STOCKS: A REVIEW

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## ABSTRACT

The instantaneous rate of natural mortality (*M*) is an important but poorly quantified parameter in most mathematical models of fish stock dynamics. This report reviews methods used commonly to estimate *M* for fish stocks, sensitivity of some common fishery models to values chosen for *M*, and evidence refuting the common assumption that a constant value can be an adequate approximation of *M* within single stocks.

With the exception of simple surplus production models (e.g., Schaefer 1954; Pella and Tomlinson 1969) all mathematical models of fish stock dynamics include as a parameter the instantaneous rate of natural mortality (*M*). The models do not require explicitly any particular form for *M*; it can be constant or can vary in any imaginable form. But because natural mortality has proved extremely difficult to measure directly, *M* is assumed almost universally to be some constant specific to whatever stock is being modeled. This is particularly true for analyses of commercial fish stocks, which often require estimates of *M* only for the postrecruit ages. Decreases in natural mortality with increasing age during egg and postlarval stages are so dramatic compared to apparent changes during postrecruitment ages (e.g., Cushing 1975) or compared to differences between different sexes, collection sites, seasons, years, cohorts, or stocks within species, that variations in *M* during these later (postrecruitment) ages are often assumed negligible.

Whether this assumption is in fact acceptable is the subject of this report. The answer is no, it is probably not acceptable in most cases. That answer follows from the information presented in Sections II through V, with the following conclusions:

Section II: Current methods for estimating natural mortality: a review of methods used currently to estimate *M* in fish populations. All of these methods have strong limitations or disadvantages.

Section III: Sensitivity of fishery models to choices for *M*: a review of the sensitivity of some standard fishery models to different choices for input value(s) of *M*. Existing studies show that the models are sensitive and that sensitivity is affected not only by the values chosen for *M*, but also by interactions between *M* and the values chosen for other parameters in the models.

Section IV: Evidence for nonconstant *M*; factors influencing death rate: a review of factors assumed or shown to affect *M* in fish stocks. Available information implies that many such factors exist, acting alone or in concert.

Section V: Evidence for nonconstant *M*; variability within and between groups: a review of existing quantitative evidence for the extent of variability in *M* between but especially *within* stocks. Because almost all fishery models focus on single stocks, variability within stocks (as opposed to between stocks) is the most important question. Some studies show strong differences between mortality rates of various groups of fish; some do not. Those which do not have tended to assume there would be none, and have often used catch curve regression analysis to derive a single estimate from data combined over many groups (usually years) of data. The few studies from which it is possible to determine ranges of estimates show differences of at least 50 to 100% between minimum and maximum estimates for single groups (e.g., stocks) of fish.

The report's major conlcusions are that natural mortality is far from constant for many fish stocks, and that this variability is extensive enough that it should not be ignored. Analyses of

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fish stock dynamics need much more rigorous estimates of **within-stock** variability (both trends and variance) in $M$ for exploited fish stocks.

## II. CURRENT METHODS FOR ESTIMATING NATURAL MORTALITY

Three methods are used currently or have been proposed to estimate $M$ in fish populations: 1) analysis of catch data, usually from commercial fisheries but also from sampling programs specifically conducted for stock assessment (this includes mark-recapture studies), 2) correlations of $M$ with other life history parameters, and 3) estimation of deaths due to predation. I describe below each method in turn, listing both advantages and disadvantages of each.

### Catch-Analysis Methods

Methods for deriving estimates of natural mortality from catch data are based on measuring decreases in abundance, either relative or absolute, in groups of fish during two or more successive periods of time. Groups may be distinguished on the basis of any identifiable characteristic, e.g., size (length or weight), age, sex, location and time of capture, or some identifiable tag or mark.

The most common grouping is by age, for two reasons. First, age has been considered historically the most important factor potentially affecting estimates of mortality rate and subsequent results from the most commonly used fishery models (e.g., Heincke 1913; Baranov 1918). This is probably because the methods were developed for temperate water fisheries which tend to have obvious annual reproductive cycles, so that individual year classes are often relatively easy to distinguish. Second, the earliest method of estimating $M$ (catch curve analysis, discussed below) depends on determining the rate during successive ages.

Regardless of the grouping criterion, methods for estimating $M$ use generally one of two types of data. The first type is simply subsamples of unmarked catch. These subsamples contain fish selected randomly and classified into groups on the basis of size (length or weight). The second type is mark-recaptures, in which previously marked individual fish can be identified and classified after recapture into groups on the basis of this positive identification. Estimates of mortality are usually derived from samples of unmarked fish by analysis of resulting "catch curves" (Ricker 1975). Because it has been used so frequently, catch curve analysis is discussed below in some detail.

With marking it is possible to follow the history of individual fish, so many different types of estimation procedures exist for deriving estimates of mortality from mark-recapture data (e.g., Ricker 1975; Jones 1979; Brownie et al. 1985). Because so many variations are possible, marking experiments are discussed only generally, stressing the basic advantages and disadvantages of marking data relative to data from unmarked samples, in deriving estimates of mortality from these data.

Size-frequency distributions from unmarked subsamples of catch (the first type of data) are converted usually to age-frequency distributions, on the basis of previously determined relationships between age and length or age and weight. Subsequent analyses concentrate on analyzing this resulting curve of age-composition (e.g., Ricker 1975). Abundance usually decreases exponentially with size (or age) in this type of sample. Converting the abundances to their logarithmic values often results in a relatively linear decrease during most exploited ages (or sizes), after some initial increase in vulnerability. Graphs of these logged-frequency distributions are usually called "catch curves", and their analysis, "catch curve analysis". "Catch curve analysis" generally consists of determining the best-fit straight line through the decreasing portion of the logged-frequency distribution, because if the decrease in abundance is truly exponential, the slope of this line through the log-transformed data is the instantaneous rate of decrease in abundance (e.g., Ricker 1975).

There are two basic types of catch curves, distinguished on the basis of when the data were collected and how many groups are represented in the curves. The first, horizontal catch curves, includes data from several groups (e.g., size or age classes) collected at a single point in time (or combined from two or more points in time). Thus, horizontal catch curves reflect "ancient history". The individuals contributing to the frequency distribution were not originally all members of the same group. To use this type of catch curve, one must assume that for each successive age, risk of mortality has been historically the same for all individuals achieving that age. If this has not been the case, the catch curves may show various types of curvature in the descending leg, but absence of curvature is no guarantee that the rates have in fact been constant.

Thus, horizontal curves are subject to the extremely restrictive assumption that the groups from which the data were collected must be in steady state relative to each other, i.e., their relative abundances must be constant through time. If this is true, then a graph of data collected at a single point in time, which may include, for example, individuals from 5 consecutive year classes displayed as frequencies at 5 consecutive ages, will look the same as the 5 graphs of data that will result from collecting samples during 5 consecutive years (ages) from each of the 5 year classes. If these conditions are not met, simple linear fitting to determine a single estimate for mortality will be inappropriate.

The second type of catch curve, longitudinal, includes data collected from a single identifiable group over a protracted period of time. Most often, this will be a single cohort of fish such as single year class, sampled during successive years. Longitudinal curves are not subject to the assumption of steady state, but do share with horizontal catch curves several other severe disadvantages. These include 1) groups must be adequately identifiable; 2) groups must be closed to migration, so that changes in abundance are due only to fishing or natural mortality, or if migration does occur, it must occur in proportion to the age distributions in the local groups; 3) samples must represent adequately the true composition of the groups in nature; 4) rate(s) of mortality must be relatively constant between groups over time, so that the log-transformed frequency distributions are truly linear (e.g., Jensen 1984); 5) compensatory relationships between stock levels and natural mortality, or fishing mortality and natural mortality, must not be present.

Methods for estimating $M$, which assume to greater or lesser degrees that the conditions listed above are met, have been described repeatedly. The methods tend to fall into two categories. Methods in the first category estimate $M$ from catch records of unexploited or lightly exploited groups of fish. In these groups, $F$ equals or approximates zero. Therefore, the observed rate of decrease ($Z$) equals or approximates $M$, because $Z$ equals the sum of $F$ and $M$ (e.g., Heincke 1913; Baranov 1918; Ricker 1947; Beverton and Holt 1957; Robson and Chapman 1961; Pauly 1982; Munro 1982; and among others).

Methods in the second category estimate $M$ by determining $Z$ at various levels of fishing effort, then using the observed relationship between $Z$ and effort to predict, via regression analysis or manipulation of various ratios, the value of $Z$ at zero effort (e.g., Silliman 1943; Beverton and Holt 1957; Paloheimo 1961; Lander 1962; Chapman and Murphy 1965; Paulik and Robson 1969; Gulland 1983; Butler and MacDonald 1979; Fournier and Archibald 1982; Caddy 1984; and others).

These methods are most appropriate for analyzing catches of unmarked fish. Accurate results depend strongly on accurate measures of catch per unit effort (CPUE) and constant catchability ($q$) because if these conditions (in addition to those listed above) are not met, observed relationships between abundances in different sample groups may not reflect true differences between groups in situ.

Marked fish present fewer problems. Advantages include 1) concentration on measuring relative rather than absolute differences between abundances of different groups, 2) immigration need not be considered, as entire original groups are known to carry marks, and 3) with sufficiently large samples, it becomes possible to test for differences in mortality rate between different groups (e.g., between ages, between sexes, or between sampling sites), rather than having to assume that such effects are negligible.

Reviews and descriptions of various mark-recapture methods appear in papers by Seber (1973), Ricker (1975), Jones (1979), and Brownie et al. (1985). Some of the newer types of marking analyses can solve many of the most vexing problems associated with traditional catch curve analysis (e.g., Reed and Davies 1980; Hochbaum and Walters 1984; Burnham and Andersen 1984; Burnham et al. 1984; Brownie et al. 1985).

Several disadvantages unique to marking operations counteract these advantages, however, even with the newer methods. These disadvantages include various types of mark-induced effects on mortality rates, behavior, and vulnerability to capture, as well as mark loss, unrepresentative mixing of marked fish with their original groups prior to recapture (e.g., Ricker 1975), and especially in commercial fisheries, underreporting or incorrect reporting of recaptures.

Both analysis of catch curves from unmarked fish and analysis of mark-recapture data have the advantage of requiring only catch (and usually effort) data, and these data can generally be collected by sampling catches from commercial fisheries. However, in addition to problems specific to each method, they have in common one or more other major disadvantages: 1) inability to distinguish between losses (or gains) from migration or recruitment versus losses due to fishing or natural causes, 2) imprecision in the estimates of $M$ obtained (e.g., Beverton and Holt 1957; Taylor 1958; Bishop 1959; Paloheimo and Dickie 1966; Ricker 1975, 1977; Doubleday 1976; Pauly 1980; Larkin and Gazey 1982; Paloheimo 1980, 1982; Myers and Doyle 1983; Roff 1984), 3) sensitivity to size-specific mortality affecting the estimated age-structure of the group (Ricker 1969), 4) errors in estimates of age, such that abundances-at-age derived from age-length conversions are unrepresentative, 5) where analyses are conducted on data combined over two or more cohorts, the unlikely condition that mortality rates were in fact similar for all cohorts, and 6) problems inherent in the analyses themselves (e.g., Barlow 1984). Disadvantages 1, 4, and 5 may not apply to marked fish. Disadvantage 5 does not apply to single cohorts. But collections from marked groups and single cohorts are still vulnerable to the other problems.

Further, although in principle it would be possible to estimate $M$ for different ages, times, or places, most commonly in practice a single, fishery-wide constant $M$ is estimated by pooling data from throughout the fishery. By implication, the analyst is assuming that the exploited stock was more or less in steady-state over all times and areas of catch so that $M$ was relatively constant while that data set was collected and while (historically) the observed age-distributions were being created. In fact, substantial evidence exists that $M$ is not constant, either within a single stock over time (age) or between stocks of a given species in different areas (Sections IV and V).

A final disadvantage is that catch-curve analyses are fundamentally unmechanistic, generated simply by charting changes in abundance. Catch-curve analyses cannot predict the effect of changes in factors that control $M$; thus there is little hope of predicting $M$ in the future should conditions change.

## Life History Methods

A second approach to estimating the instantaneous rate of natural mortality in fish stocks is based on the observation that $M$ often correlates strongly with life history parameters, such as growth rate, age at sexual maturity, costs of reproduction, and maximum age (Table 1).

Typically in such studies, analytical formulas are derived from theoretical relationships between the various parameters (e.g., Beverton 1964), or empirical formulas are derived from regression of $M$ against one or more of the parameters (e.g., Hoenig 1983). These models have two significant advantages: 1) they require minimal amounts of data, and 2) they are useful in demonstrating broad trends across species and in developing ecological theory. But because they produce only a single and often very imprecise estimate of $M$ for any given group of fish, they are not particularly effective for generating precise estimates of natural mortality or for determining the existence or extent of trends and variability in $M$ for given stocks. They will also be no better than the methods used to estimate the values of $M$ used in the regressions.

TABLE 1.—Studies relating instantaneous rate of natural mortality to life history traits in fish.

| Traits | Species | Source |
|---|---|---|
| $^{1}T_{max}$, $^{2}k$, $^{3}L_{inf}$, metabolic rate, reproduction | Various | Beverton and Holt 1959 |
| $T_{max}$, $k$, $L_{inf}$, $^{4}L_{asm}$, fishing | clupeids, engraulids | Beverton 1963 |
| $^{5}W_{inf}$ | general | Ursin 1967 |
| $T_{max}$, $^{6}T_{max.biomass}$, $k$, | general | Alverson and Carney 1975 |
| growth rate | young fish | Ware 1975 |
| $L_{asm}$, gonad size, condition factor | gadoids | Jones and Johnston 1977 |
| $T_{max}$ | general | Blinov 1977 |
| gonad/body weight index, $^{7}ASM$, $T_{max}$, $L_{inf}$ | general | Gunderson 1980 |
| $W_{inf}$, $L_{inf}$, $k$, water temperature | 175 stocks | Pauly 1980 |
| energy cost of reproduction | general | Myers and Doyle 1983 |
| $T_{max}$ | various | Hoenig 1983 |
| weight | various | Peterson and Wroblewski 1983 |
| $k$, $L_{inf}$, $L_{asm}$ | various | Roff 1986 |

[1] Maximum age,
[2] Von Bertalanffy growth parameter.
[3] Maximum length.
[4] Length at age of sexual maturity.
[5] Maximum weight.
[6] Age at occurrence of cohort's max biomass.
[7] Age of sexual maturity.

### Predation Methods

A third class of estimators extends single species cohort analysis to a multispecies assemblage incorporating the major predators and alternative prey of the stock in question. Single species cohort analysis is used to estimate population abundances and annual values for the instantaneous rate of fishing mortality (*F*) for single groups, usually year classes, of fish (e.g., Pope 1972; Ricker 1975; Gulland 1983). The multispecies extension simply combines cohort analyses for several species (e.g., Anderson and Ursin 1977). The methods all generate estimates of *M* as the sum of some constant rate of nonpredatory, nonfishing mortality plus the total estimated flux of prey (stock) to each of the major predators. This feeding flux to predators is estimated by first using cohort analyses to reconstruct population sizes of the various groups of predator and prey, then combining these population sizes with observed growth rates for the predators and with estimated preferences for various prey. Thus it becomes possible to estimate the predatory component of *M*.

Versions of the method have been described by Anderson and Ursin (1977), Majkowski (1981), and Pope and Knights (1982). Applications in a marine system (North Sea) have been described by Anderson and Ursin (1977), in an ecosystem context, by Laevastu et al. (1982) and in lake systems by Forney (1977) and Stein et al. (1981).

The predation method has been developed primarily from analyses of marine systems, especially the North Sea, and much of the literature exists only as "mimeos" or notes associated with ICES (International Council for the Exploration of the Seas) activities. The most readily available discussion of this approach appeared in Mercer (1982), which includes a critical review and discussion by Ursin (1982) of the various methods. Several other discussions appear in Pauly and Murphy's (1982) volume of collected papers from a symposium on theory and management of tropical fisheries. Most of these papers specifically address tropical multispecies systems, but the concepts are broadly applicable. References to other, often less accessible, works can be found in these two general references.

The predation method is elegant in concept but often difficult to apply. Studies by Forney (1977) and Stein (1981) had the distinct advantages of limited species numbers in a small system, and direct quantification of stomach contents. Yet even in lake systems, the sampling problems of estimating *Z*, population abundances, and so forth, remain often as intractable as in large marine systems. The two greatest problems are 1) the difficulty in defining vulnerability and preference functions for the various prey stocks (e.g., Ursin 1982) and 2) the need to include cohort analyses of all the major interacting species, some or many of which may not be available commercially (and for which therefore data will be scarce).

Despite these problems the approach can certainly generate, for stocks that suffer heavy predatory mortality from other fished stocks, more realistic estimates of *M* than approaches that simply generate a globally fixed and invariant *M*. More importantly (and in contrast to the age-frequency or life history methods) the predation method has the advantage of being mechanistic. Predation-related causes and consequences of age, size, site, stock, geographic, or time trends in *M* can be investigated via perturbation and sensitivity analysis in computer simulation studies or, alternatively, investigated through analysis of existing catch data. It becomes possible (not necessarily feasible) to investigate the implications of varying age or abundance structures of interacting fishery resources.

Thus the predation approach has considerable conceptual appeal for fairly simple systems in which 1) predation is the major force controlling prey abundance, 2) predators have few alternative prey, 3) the possibility can be ignored that predators prefer moribund prey which were about to die anyway, and 4) all major species of predator and prey are sought commercially so that data on abundances and feeding preferences are or can be made available.

Unfortunately, the number of systems satisfying these requirements appears to be fairly small, and of course where predation is a relatively small fraction of *M*, the multispecies predation method will be particularly ineffective.

## III. SENSITIVITY OF FISHERY MODELS TO CHOICES FOR *M*

Although catch-analysis, life history, and predation methods all exist currently for estimating *M* in fish stocks, in practice the only method used extensively is the first—direct estimation of *M* from analysis of catch structure. Thus the discussion below of model sensitivity to *M* is based on this type of estimate. The conclusions reached are not specific to this one method. Model sensitivity to a given derived value of $M$ will be the same, regardless of the method used to derive the value.

## General Patterns

Sensitivity analyses of $M$ in fishery models have evolved through two phases. Earlier studies noted the influence of $M$ on estimates of maximum yield ($Y_{\max}$) or maximum yield per recruit ($(Y/R)_{\max}$), and on $F_{\max}$ (the fishing pressure required to produce maximum yield) in Beverton-Holt yield models (Beverton and Holt 1957; Hennemuth 1961; Francis 1974; Parks 1977; Bartoo and Coan 1979; Bulgakova and Efimov 1982). More recently, as cohort analyses have become more popular, more attention has been directed toward assessing the influence of $M$ on age-specific estimates of stock sizes ($N_i$) and fishing mortalities ($F_i$) produced by these models (Murphy 1965; Pope 1971; Ricker 1971; Agger et al. 1973; Doubleday 1976; Ulltang 1977; Doubleday and Beacham 1982; Pope and Shepard 1982; Sims 1982a, 1982b, 1984). A few other studies have investigated the effect of $M$ on estimates of maximum sustainable yield (MSY) or total biomass (Francis 1976; Deriso 1982; Beddington and Cooke 1983; Tyler et al. 1985).

Most of these studies have used a single, invariant value for $M$. Model sensitivity is then assessed by comparing model results using some "best" estimate of $M$, to results using one (or rarely, more) pair(s) of $M$ values some arbitrary percentage above and below the best estimate. Only a few studies exist of the effects of nonconstant $M$, where $M$ varies in different groups of fish within a given stock. These include Beverton and Holt's (1957) example of density-dependent $M$ in plaice, and several investigations of age-specific $M$ (Parks 1977; Ulltang 1977; Bartoo and Coan 1979; Sandland 1982; Bulgakova and Efimov 1982; Caddy 1984; Tyler et al. 1985).

No study to date has specifically addressed the problems of estimating values of $M$ for a full fishery analysis, leading from cohort analyses (using $M$ to estimate $F_i$, $N_i$, and recruitment $R$) to estimates of yield or yield-per-recruit using the same $M$(s) and $R$ subsequently in the Beverton-Holt formulas. Also, no study to date has addressed the possibility and consequences of differing patterns of variability in $M$, although it has been suggested in one case (Ulltang 1977) that random variations will be unimportant if the rate is constant (on average) over the fished ages.

In general, the earlier analyses with yield models assuming a constant $M$ show that *higher* estimates of $M$ lead to 1) **lower** estimates of $Y_{\max}$ or $(Y/R)_{\max}$ (because fewer survive to be caught), 2) *higher* estimates of $F_{\max}$ (you must fish a bit harder to catch a given amount of those left), and 3) **lower** estimates of age at first capture ($t_c$; because it pays to catch them before they die, rather than waiting for them to grow bigger but less abundant).

Including density-dependence tends to exaggerate these trends, at least for plaice in the North Sea (Beverton and Holt 1957). Including age-structured $M$ in yield models also affects the estimates, but not necessarily in a straightforward manner. As described below in the section on numeric results, change in model output for a given change in $M$ depends not just on the values chosen for $M$, but also on those chosen for the other parameters. $M$ is not an independent parameter in these models.

Analyses with cohort or virtual population models which assume a constant value for $M$ show that in general the effect of increasing $M$ is to increase estimates of $N_i$ (because the higher $M$ is, the more fish died in addition to those being caught) and to decrease estimates of $F_i$. The data show only $Z$, which is the sum of $M$ and $F_i$. Assuming $Z$ has been constant, a decrease in $F_i$ requires an increase in $M$. If $Z$ has been variable, the lower $F_i$ may be explained on the basis of higher $N_i$, a smaller proportion of which ($F_i$) would account for the observed catch.

The actual effect, particularly on estimates of $N_i$, is not necessarily that simple. As with yield models, a given change in $M$ does not always produce the same change in model output. The result depends also on values chosen for other parameters; $M$ is not an independent parameter.

In cohort analysis the results (estimates of $N_i$ and $F_i$) are particularly sensitive to the relative sizes of $F$ and $M$ (i.e., to the exploitation ratio $E = F/(F + M)$). The effect of assuming an incorrect value (or series of values) of $M$ tends to build up as the analysis proceeds backward in time. This is because with every time step backward the catch ($C$) is inflated by the factor $M$ in order to estimate at that time the size of the entire stock, not just the size of the catch. That is

$$N_i = N_{i+1} + C_i(F_i + M)/F_i \qquad (1)$$

where $F_i$ satisfies the catch equation

$$C_i = N_{i+1} \, (F_i/F_i + M) \, (e^{(F_i + M)t} - 1) \qquad (2)$$

If $M$ is large relative to $F$ (i.e., the exploitation ratio is low), then errors in $N_i$ can increase progressively and become quite large at the younger ages (e.g., Agger et al. 1973; Murphy 1965; Ulltang 1977; Sims 1982a, 1982b, 1984).

## Numeric Results

Although general responses of various models can be determined simply by inspection of the analytic models themselves, the quantitative change to expect in the result (output) for a quantified *change* in $M$ (input) is not always immediately obvious. This is because $M$ tends to occur more than once in various formulas. For example, $M$ appears in both the numerator and denominator in the solution to the Beverton-Holt yield equation (Ricker 1975).

$$\begin{aligned} Y = FN_0e^{(-Mr)}W_{\infty}(1/(M + F) \\ - 3e^{(-kr)}/(M + F + k) \\ + 3e^{(-2kr)}/(M + F + 2k) \\ - e^{(-3kr)}/(M + F + 3k)). \qquad (3) \end{aligned}$$

So, rather than derive analytical expressions (e.g., Sims 1984), I resort below to a simpler approach. Sensitivity of fishery models to changes of given magnitude in $M$ is assessed by comparing percent change reported in model response (output) to percent change in $M$ (input). In cases for vector (age or density-dependent) $M$, I have merely described the shape of the $M$-vector. For these different vectors, I report the percent change in the result due to switching from a vector of one shape to a vector of another shape.

### Yield Models

At least four studies (Beverton and Holt 1957; Hennemuth 1961; Francis 1974; Bartoo and Coan 1979) have shown that errors in estimates of $M$ propagate into roughly equal errors in estimates of $(Y/R)_{\max}$, but with sign reversed (Table 2). For example, a 10% overestimate in $M$ will lead to approximately 10% underestimate of $(Y/R)_{\max}$. An equally important result is that the actual magnitude of the effect induced depends strongly not just on the error in $M$, but on the values chosen for the other parameters in the model.

In another study, Beddington and Cooke (1983) used the Beverton-Hol formulation to investigate the influence of $M$ (constant; 0.1 to 0.8 year$^{-1}$), $t_c$ (0 to 4 years), and $K$ (the von Bertalanffy growth parameter; 0.1 to 0.5 year$^{-1}$) on MSY (maximum sustainable yield), expressing the result as "MSY as a % of $B_0$," where $B_0$ is the initial or recruited biomass. Higher percentages indicate that more of the original biomass is being taken at MSY. Increasing $M$ by a factor of 8 (0.1 to 0.8 year$^{-1}$) increased MSY/$B_0$ by a factor of about 4 to 8, depending on the particular values of $t_c$ and $K$. Again, errors in $M$ produced roughly the same relative error in the result; and again the actual effect of any given change in $M$ de-

TABLE 2.—Sensitivity of estimated maximum yield per recruit ($(Y/R)_{\max}$) to changes in instantaneous rate of natural mortality ($M$) and other input conditions. Sensitivity of $(Y/R)_{\max}$ and of changes in $M$ are expressed as percentage difference from nominal responses at nominal (best-guess) $M$. Symbols are: $t_c$ = age-at-first-capture, $F$ = instantaneous rate of fishing mortality, $M$ = nominal value for $M$. Frances (1974) used an age-structured simulation model. All other citations used standard yield-per-recruit analyses.

| Input conditions | % change in $M$ | % change in $(Y/R)_{\max}$ | Species | Source |
|---|---|---|---|---|
| $t_c$ = constant (3.72)<br>$F$ = variable<br>$M$ = 0.10 | +50<br>−50 | −20<br>+30 | plaice | Beverton and Holt 1957 |
| $t_c$ = variable<br>$F$ = constant (0.73)<br>$M$ = 0.10 | +50<br>−50 | −60<br>+50 | plaice | Beverton and Holt 1957 |
| $F$ = constant (0.95)<br>$M$ = 0.8 | +20<br>−20 | −21<br>+32 | yellowfin tuna | Hennemuth 1961 |
| $M$ = 0.8 | +10<br>−10 | −14<br>+16 | yellowfin tuna | Francis 1974 |
| $M$ = 0.60 | +25 | −20 | yellowfin tuna | Bartoo and Coan 1979 |

pended on the values chosen for the other parameters.

Pope and Garrod (1973) present another example of sensitivity in MSY to values chosen for $M$. They describe briefly the consequences of using an incorrect constant for $M$ of cod stocks when estimating the $F$ required to generate MSY ($F_{\mathrm{MSY}}$). Underestimating $M$ by 50% (assumed $M = 0.1$ year$^{-1}$; true $M = 0.2$ year$^{-1}$) leads to a choice of $F_{\mathrm{MSY}}$ that is 67% too high. Overestimating $M$ by 50% (assumed $M = 0.3$ year$^{-1}$, true $M = 0.2$ year$^{-1}$) underestimated $F_{\mathrm{MSY}}$ by 50%.

The simulations described above tested the effects of choosing alternative constant values for $M$. Choosing a vector alternative can also have significant effects; again, the magnitude of the effect depends on the values chosen for other parameters. Beverton and Holt (1957) showed that incorporating density-dependence in $M$ for plaice decreased $(Y/R)_{\max}$ by 12%, when holding $t_c$ constant at 3.72 years and letting $F$ vary. Conversely, holding $F$ constant and letting $t_c$ vary decreased $(Y/R)_{\max}$ by about 37%.

Age-dependent values for $M$ were compared with age-constant values by Bartoo and Coan (1979), Bulgakova and Efimov (1982), and Tyler et al. (1985). In their analysis of Atlantic yellowfin tuna stocks, Bartoo and Coan found that replacing an assumed constant $M$ of 0.8 year$^{-1}$ with an age-structured $M$ increasing from 0.1 year$^{-1}$ at age 0 to 1.2 year$^{-1}$ at age 7, increased $(Y/R)_{\max}$ by 17% (from 6 to 7 kg).

Estimating total yield ($Y_t$) rather than ($Y/R$) and estimating $R$ as a function of constant versus age-specific $M$ in analysis of catch curves for relatively unexploited stocks of Pacific ocean perch and Oregon hake, Bulgakova and Efimov (1982) found that replacing a constant (age-averaged) $M$ with age-variable $M$ tended to increase estimated $Y_t$ when fish recruited fairly late to the fishery, but decreased $Y_t$ if the fish recruited early. This is because of the interaction between the values assumed for $M$ (constant or age-variable) and the value calculated for $R$ from each type of mortality curve.

Starting with a given value for recruitment at age 6 years (from Efimov 1976), they calculated $R$ twice for ages 4 and 8 years—once with age-averaged $M$ and once with age-specific $M$. Because in this set of data the age-averaged $M$ was generally higher than the age-specific $M$ at the tested ages of recruitment (ages 4, 6, or 8 years), back-calculations with age-averaged (i.e., constant) $M$ predicted fewer recruits than back-calculations with age-specific $M$. With fewer recruits and generally higher $M$, potential yield at later ages obviously must drop. Differences in predicted potential yield ranged from about −30% at $t_4$ (age-specific estimate lower than age-averaged estimate, when fish were assumed to recruit to the fishery at age 4 years) to +15% at $t_6$ (age-specific estimate higher) and to +60% at $t_8$.

Tyler et al. (1985) tested (among other things) the effects of ignoring "true" age-structure in $M$ and using instead a constant value in estimating stock biomass using Deriso's (1980) delay-difference model. They did the tests on catch data generated by Walter's (1969) age-structured simulation model of cod, using three different (input) age structures for $M$ in Walter's model. After generating "catch data" from Walter's model, they analyzed the simulated data set using Deriso's model with constant $M$ (= 0.5 year$^{-1}$). The age structures tested were 1) mortality increasing and then decreasing with age (Walter's original mortality vector spanning ages 3 to 12 years; age-averaged $M = 0.55$ year$^{-1}$, range = 0.33 to 0.70 year$^{-1}$), 2) mortality increasing with age (ages 7 to 12 years; average $M = 0.5$ year$^{-1}$, range 0.3 to 0.7 year$^{-1}$) and 3) mortality decreasing with age (ages 7 to 12 years; average $M = 0.5$ year$^{-1}$, range 0.7 to 0.3 year$^{-1}$). In all three cases Deriso's model with constant $M$ misestimated the "true" biomass generated by Walter's model (with age-structured values for $M$). The differences were relatively small, however: −13% for the increasing and then decreasing series, +19% for the decreasing series, and +4% for the increasing series. These differences were due to the differences in $M$, and not the differences in model structure; generating and analyzing biomass with the same constant $M$ in both models led to a discrepancy of only 0.5%.

By analogy to life history patterns in other adult animals, $M$ (after recruitment into most fished stocks) is more likely to increase with age than to cycle or decrease. By implication, the simulation results from the increasing series are probably most realistic. If so, the effects of ignoring age-structure in favor of using a constant $M$ may be relatively small (5 to 20%), at least for the cod stock simulated in this study. But the results obviously depend again not just on correctly choosing the values for $M$, but on the values chosen for the other parameters. In this case, Tyler et al.'s (1985) results imply that age-structure in $M$ can be relatively unimportant, at least when the assumed constant is evenly bracketed by the "true" age-structure in *M*.

Further simulations by Tyler et al. (1985) using a wide range of constant values for *M* (0.4 to 1.4 year$^{-1}$) and the growth rate parameter rho (mean Ford growth coefficient for the fishable stock; 0.46 to 1.6) showed that incorrect guesses of *M* (and rho) could produce errors up to 1,000% in estimated biomass. More realistic ranges for the two parameters (0.4 to 0.8 year$^{-1}$ for *M*, 0.6 to 1.2 for rho), extending about 50% above and below the "true" values for these parameters, induced much lower error in biomass estimates (about the same order of magnitude, 50 to 100% below and above the "true" biomass). As before, changes (errors) of a given amount in *M* (expressed as fraction or percentage of the original value) appear to produce about the same amount of change (expressed as percent of original value) in simple estimates of yield, depending on the conditions of other parameters in the model.

Chatwin (1958) compared estimates of $Y_{\max}$ from lingcod populations. Rather than compare constant and age-variable values for *M*, he assumed several different values for an average (constant) *M* in adults, but assumed that *M* increased from the assumed average for adults to higher values in both juveniles and senescent fish. He reports no quantitative results but states, as found above, that increasing the average *M*, for a given *F*, considerably decreased $Y_{\max}$, that decreasing *M* increased $Y_{\max}$, and that size at first capture changed relatively little with those changes in *M*.

These comparisons between age-structured versus constant *M*, or between different constants have demonstrated that effects on results can be large for some combinations of parameters yet small for others. Alternative choices drawn from apparently realistic parameter values lead to relatively small differences in estimates of *M*. Specific amounts of change depend strongly not only on the values chosen for *M*, but also on the value of *M* **relative** to values chosen for the other interacting parameters in the yield models. For most choices of parameter values, sensitivity of output is roughly equal to perturbation of input.

### Cohort Analyses

Effects of interactions between changes in *M* and values chosen for other parameters is even more obvious in stock reconstruction analyses (e.g., cohort analysis and virtual population analysis (VPA)). These analyses are used to "reconstruct" estimates of stock abundance during previous years, based on catch data and assumptions about the value(s) of *M* during those previous years. Studies of sensitivity to *M* in Beverton-Holt types of yield or biomass assessments were usually empirical, based on analyses of catch data from specific fisheries. Studies of sensitivity to *M* in VPA and cohort analysis include both theoretical and empirical studies; i.e., simulations using totally contrived data sets (e.g., Agger et al. 1973), analyses of specific data sets (e.g., Pope 1971; Doubleday and Beacham 1982) and combinations of analytical evaluations and analysis of specific data sets (e.g., Doubleday 1976; Ulltang 1977; Sims 1982a, 1982b, 1984).

Simple analyses of sensitivity to *M*, in which *M* is varied but all else is held constant, include 1) Pope's (1972) analysis of Atlantic yellowfin tuna, in which he found that replacing constant *M* with age-structured *M* (higher *M*s for older fish) produced lower estimates for fishing mortality ($F_i$) in the later ages, but had little effect on estimates for the younger ages, and 2) Doubleday and Beacham's (1982) statement that 10% error in constant *M* translated into 9 to 14% error in estimates of *R* (at age 3) for cod in the Gulf of St. Lawrence.

Somewhat more complicated analyses are presented by Ulltang (1977) and Sims (1982a, 1982b, 1984). Ulltang evaluated the effects on model predictions of $F_i$ and $N_i$, of several types of variation in *M*. These included no variation (uniformly constant *M*), *M* constant within years but varying randomly between years, *M* varying with age, and *M* varying with season. Sims evaluated the effects of choosing various constants for *M* on estimates of $N_i$, and derived an analytical expression relating variance in *M* to expected variance in estimates of abundance.

In Ulltang's simulations, increasing (decreasing) a constant *M* by 50% (from 0.2) decreased (increased) *F* by about 20% ("true" *F*'s ranging from 0.4 to 0.8). Creating a data set with *M* varying randomly from one year to the next, then analyzing those data with an assumed constant *M*, Ulltang (1977) found that the *Z* calculated from the constant-*M* model was on average the same as the "true" *Z* from the random-*M* model. He concluded that random fluctuations in *M* will cancel out during analysis and so can be ignored. Ulltang assessed the influence of age-dependent *M* compared with constant *M* by generating a catch curve with age-variable *M* (decreasing curvilinearly from 0.3 at age 1 to 0.1 at age 10, average about 0.2) and $F$ equal to 0.2, then analyzing the catch with $F$ equal to 0.2 or 0.6, and $M$ equal either to 0.1 or 0.2. Choice of $M$ made little difference in estimates of stock size for the case of high $F$ (0.6), because most of the deaths were due to (observed) fishing. When $F$ was low (0.2), stock-size estimates were much more sensitive to incorrect choices for $M$, because most of the deaths were due in this case to $M$, which was unmeasured and therefore unobserved.

Ulltang (1977) simulated seasonal changes in $M$ by concentrating all deaths in either the first or last quarter of a year. Estimated stock sizes ($N_i$) changed relatively little; with $F = 1.2$ and $M = 0.4$, $N_i$ was a maximum of 10% higher if all deaths occurred first quarter, 10% lower if all occurred in the last quarter.

A serious problem with the conclusions reached by Ulltang (1977) is also common to all the other studies discussed above; they are based on relatively few combinations of values for the various parameters, and relatively few simulations. For example, the conclusion that random errors in $M$ will tend to even out is intuitively attractive, provided the time scale of variation is short relative to the generation time of the fish. In fact random variation in $M$ did even out in the two sets of simulations he conducted. But the examples he chose included only one set of ages (2 to 10 years), with relatively high values of $F$ (0.5 to 0.8 year$^{-1}$) compared to the values tested for $M$ (0.1, 0.3 year$^{-1}$). The gravity of consequences from choosing an incorrect $M$ depends very heavily on the size of $M$ **relative to** the size of $F$, i.e., on $E$. Had he chosen different values for his simulations, he might have reached very different conclusions. This is probably the basis for the discrepancy between Ulltang's conclusion that seasonal effects are minor, versus Sims' (1984) conclusion that seasonal effects can be quite large, if $M$ is high.

Sims (1984) attempted to overcome this problem (trying to draw general conclusions from the results of simulations based on particular, or relatively few, sets of parameters) by analytically deriving formulas for relative error in stock-size estimates, and then testing the formulas with data from actual fisheries. He used this approach twice: once to assess the effects of seasonality (Sims 1982a) and once to consider in general the effects of different choices (errors) for constant $M$ (Sims 1984). But his results (and equations for error) show clearly that error in estimated stock sizes depends on several parameters and that the effects of one can be strongly dependent on the values chosen for the others. Choosing a high $M$ (0.6 year$^{-1}$) and concentrating catch during the first quarter of the year overestimated $R$ by 20%; concentrating catch during the last quarter underestimated $R$ by 23% (compared with the 10% error found by Ulltang).

Within the same analysis, reducing $M$ by half (to 0.3 year$^{-1}$) reduced the error in $R$ by half, but the same reduction of error in $R$ was also achieved by leaving $M$ high and reducing $F$. In assessing specifically the effects of error in $M$ on error in $R$, Sims (1984) showed very different effects on estimates of $R$ in heavily fished versus lightly fished cohorts of Atlantic bluefin tuna. Changing $M$ by 50% led to changes in estimated $R$ of 60 to 260% in the lightly fished cohort, but only to relatively smaller changes of 35 to 70% in the heavily fished cohort. Again, the magnitude of the error in model predictions depended not just on the magnitude of $M$, but on its relationship to the other parameters in the catch equation, particularly $F$.

Errors (expressed as percentage change in output for a given change in input) in model output in the simulations described above, all of which tried to use apparently realistic values for model parameters, rarely exceeded 50%, and were often less than the error introduced into values chosen for $M$. By implication, the effects of incorrectly guessing $M$ may be relatively unimportant if $M$ is relatively small (e.g., in this situation not more than about 0.5 year$^{-1}$) and relatively invariant, although the actual magnitude of effect due to any given percentage change in $M$ depends on the values chosen for other parameters.

So, inaccurate estimates of $M$ might be important or they might not. It all depends on the magnitude and variability of $M$ within a **given stock** (or group). Although untested, it seems likely that estimates of $M$ for groups in which $M$ varies little and is relatively low, are more likely to be reasonably accurate than estimates of $M$ from groups in which $M$ is large and variable. The following section reviews evidence that $M$ does in fact vary both within and between groups of fish, and the succeeding section reviews evidence for the magnitude of that variability in ostensibly similar groups.

## IV. FACTORS INFLUENCING DEATH RATE

Despite the fact that in most fishery models, $M$ is assumed to be constant for all exploited ages in any given stock, abundant evidence exists to the contrary. Natural mortality has been shown to vary with age, density, disease, parasites, food supply, predator abundance, water temperature, fishing pressure, sex, and size. Evidence for relationships between these factors and $M$, and selected references for each, are presented below.

Changes in mortality rate with **age**, within single groups of fish, have been demonstrated and discussed more frequently than changes with any other factor. References include, among others, Baranov (1918, plaice), Sette (1943, Atlantic mackerel), Ricker (1945, 1947, lake fish; 1969, 1975, various species), Beverton and Holt (1959, many species of marine fish), Beverton (1963, engraulids and clupeids), Boiko (1964, sturgeon), Cushing (1975, plaice), Blinov (1977, fish in general), Bulgakova and Efimov (1982, Oregon hake and sea perch), Sandland (1982, fish in general), Smith (1985, clupeoids), Roff (1986, fish in general). Evidence for changes with senescence for fish in general has been discussed or documented by, among others, Woodhead (1979) and Craig (1984).

Although specific patterns vary with species (e.g., Woodhead 1979), in general $M$ is extremely high during egg and larval stages (e.g., 2 to 10% per day in plaice and clupeoids (Cushing 1975; Smith 1985)), falls precipitously during the juvenile period, becomes **relatively** stable during intermediate adult ages and increases again with senescence. But even during these relatively stable mid-adult ages, changes in $M$ with age can be substantial, particularly in short-lived fish (e.g., Ricker 1947, stunted versus "normal" whitefish).

Changes in natural mortality rate with **size** (rather than age) within single groups of fish (usually stocks), have been discussed by Baranov (1918, plaice), Ricker (1969, size-selective mortality in general), Ware (1975, larval fish), and Peterson and Wroblewski (1984, many species). Differences in natural mortality rate between populations of the same species in different environments, or even in different areas of a single environment (e.g., a single lake) are documented by Ricker (1947), Kennedy (1954), and Schupp (1978). Year-to-year differences in natural mortality rates of single stocks from a given area are shown by Pope and Knights (1982, plaice) and by Henderson et al. (1983, whitefish). Density-dependent changes in $M$ are discussed by Beverton and Holt (1957), Cushing (1967), Tyler and Gallucci (1980), Backiel and LeCren (1978), Jones (1982), and others. Differences in $M$ between sexes have been documented by Beverton and Holt (1957, plaice), Ricker (1947, rock bass), and others. Changes in natural mortality rate related to the cost of reproduction have been discussed by Jones and Johnston (1977), Roff (1984), and others.

Other factors that affect $M$ either alone or in combination with other factors include disease and parasitism (reviewed by Lester 1984), starvation (Hewitt et al. 1985; Theilacker 1986: larval anchovy), physiological state (Smith 1985), and fishing pressure (Ursin 1982; Munro 1982). Additional examples are cited by Beverton and Holt (1957), Anderson and Ursin (1977), Sissenwine (1984), and Hunter (1984).

Most of the factors listed above (e.g., age, size, sex) are indirect influences on $M$. The most important factor directly affecting natural mortality rate is probably predation; this is implied by a large body of literature describing changes in prey community composition and abundance following changes in composition and abundance of predators (e.g., Carpenter et al. 1985).

Direct evidence that predators account for most natural mortality in fish stocks is difficult to gather (Section II). To quantify the fraction of $M$ due to predation, one must know, not only relative changes in abundance, but absolute population density of all predators and prey together with consumption rates and prey preferences of all the predators. Although this is rarely possible, at least two studies from freshwater systems do present quantified estimates of predatory mortality in relation to available prey. Forney (1977) quantified predation mortality in a relatively simple, unmanipulated lake system where there were few species of predator and prey. Combining stomach-content estimates of prey consumed with trawl-sample estimates of predator and prey abundance, he concluded that 30 to 100% of yellow perch production was consumed by walleye, their principal predator. In a manipulated system, Stein et al. (1981) assessed predatory mortality of young tiger muskellunge after they were stocked in a small pond and lake. During the time of the study, a single predator (largemouth bass) accounted for 25 to 45% of losses to natural mortality.

In marine systems evidence for the relative importance of predation can be gleaned from comparing total natural mortality with estimated predatory mortality based on abundance of predators and feeding preferences. For example, multispecies cohort analyses reported by Pope and

Knights (1982) show predatory mortality as 80 to 90% of *M* for age-0 cod, whiting, and haddock in the North Sea (the fraction of *M* due to predatory mortality cannot be assessed accurately in the older ages because predators appropriate to these sizes were not included in the analysis). In another example, estimating *M* from energy flow models, Sissenwine (1984) demonstrated that predation in the Georges Bank ecosystem can account for all production by prey fish; nonpredatory mortality was negligible.

Thus a multitude of factors, acting alone or in concert, can be expected to produce variations in *M* between individuals within single groups of fish, as well as between groups. Differences can be expected between species, between stocks within species, and from place-to-place and time-to-time within given stocks. In the following section, I will review more completely existing evidence for, and the extent of, this expected variability in *M*.

## V. VARIABILITY WITHIN AND BETWEEN GROUPS

As discussed above (Section III), simulation studies generally show that effects of choosing a particular value or set of values for *M* can range from insignificant to considerable, depending in part on the model used, in part on the values chosen for other parameters, and in part on the form chosen for the estimate(s) of *M*. Authors suggest that in the future, simulations should be conducted with a range of values for *M*, to bracket probable values (e.g., Beverton and Holt 1957; Tyler et al. 1985).

The problem with this advice is identifying the appropriate range and distribution of *M* for any given group of fish. Obviously, wide ranges for *M* will lead to great discrepancies between model predictions based on one end of the range or the other. It has been shown above, however, that model output can be relatively **insensitive** to small changes in *M*. This is particularly true if *F* is much larger than *M* (i.e., if the stock is highly exploited so that losses to fishing far exceed losses to natural mortality). The problem is determining whether, for a given stock in situ, changes in *M* are in fact large or small. Compensatory changes in *M*, in response to changes in *F*, will further confound the problem, because variations in *M* will then be a function of the value(s) of *F*, in addition to the suite of other factors that may be affecting estimates of *M*.

*M* does appear to vary considerably **between** groups of fish. Estimates of *M* compiled by Pauly (1980) (Fig. 1) for 175 stocks and species of fish worldwide differ greatly between groups, ranging from a minimum of about 0.1 $\text{year}^{-1}$ to several unusual values as high as 7.0 $\text{year}^{-1}$. Even within a group as ostensibly homogeneous as the tunas, the range of estimated mortality constants spans the majority of the common values (0.2 to 2.0 $\text{year}^{-1}$, Murphy and Sakagawa 1977).

Estimates of variability in *M* **within** groups of fish are much less common, but are actually more important than the obvious differences between groups with obviously different characteristics such as differing lifespans. Most fishery analyses are directed toward understanding or predicting dynamics of single stocks (single groups of fish). The most important considerations for natural mortality parameter values in these single-species analyses are whether and if so over what values *M* varies for the group of fish in question.

But measuring trends or variability in natural mortality rates **within** given groups (e.g., stocks) is difficult and, with the exception of trends with age, rarely attempted. This is primarily because the only extant methods for estimating *M* depend either directly or indirectly on analysis of catch data (Section II), and catch data are prone to many well known (but largely unsolved) problems.

Problems with analysis of catch data fall into two general categories: 1) problems with sampling procedure, such that fish are caught or counted out of proportion to their true abundance and 2) problems with fish appearing or disappearing from the "unit stock" due to causes other than birth or natural mortality (i.e., migration, fishing mortality, or tagging mortality), again resulting in catch data that do not represent the true structure of the stock. If sampling biases can be overcome, the problem reduces to partitioning total disappearance of fish into fractions owing to fishing, tag mortality, and migration. The first partition can be eliminated by studying unfished populations, the second by quantifying tag mortality, and the third by studying only closed or tagged populations.

Unfortunately, very few sampled populations satisfy completely even one of these criteria. Regardless, we still need at least some crude estimates of *M* in order to determine whether *M* truly varies enough to invalidate the standard assumption in fisheries models that *M* is effectively constant during exploited ages. The question here

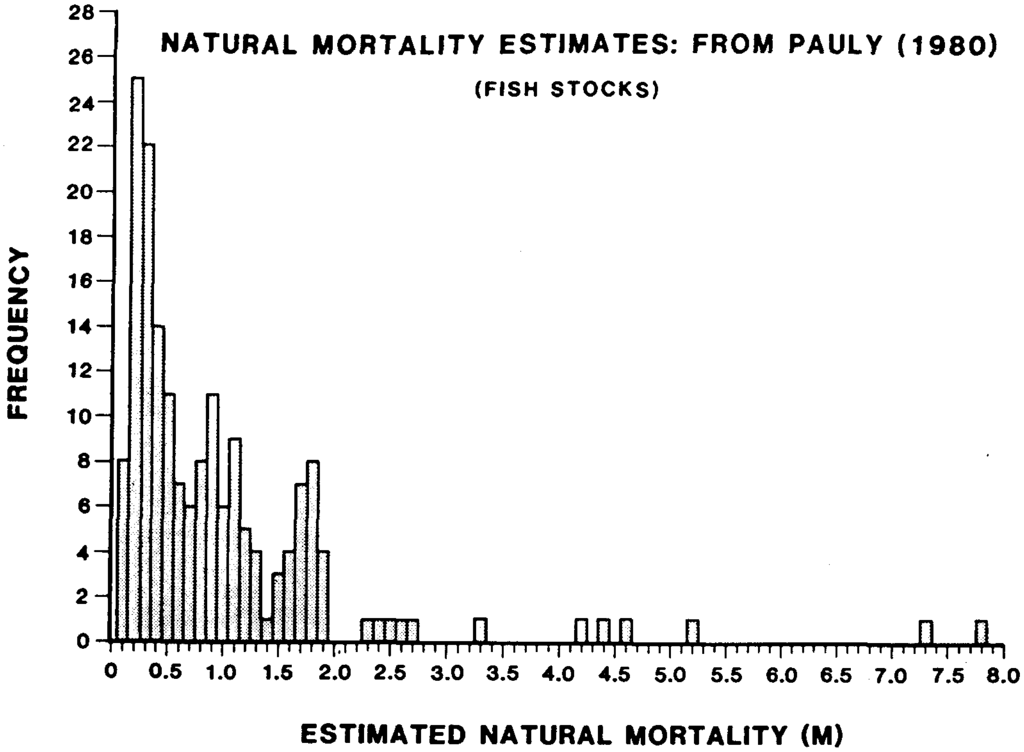

FIGURE 1.—Frequency of estimated instantaneous annual rates of natural mortality (M) in 175 different fish stocks, populations, or species. Estimates include both freshwater and marine species. Data from Pauly 1980.

concerns variability of $M$ **within** groupings that would be used commonly to estimate $M$, such as stocks of single species, rather than general patterns across species. If $M$ truly varies relatively little during these ages (so that the log of catch-at-age decreases linearly with age), if the age structure has been relatively constant historically (so that catch curves are actually linear, rather than curvilinear as seen in stocks with inconstant age structure, e.g., chapter 2, Ricker 1975), and if catch curves actually reflect relatively accurately this constancy and low variability, then most estimates of $M$ derived from analysis of appropriately processed catch curves cannot help but be relatively close to the true rate. Model predictions, although in theory sensitive, would in practice be fairly robust to any particular value chosen from the true range of values for $M$.

Despite the potential problems with accuracy or precision of existing estimates from single groups of fish, I list in Table 3 most of the estimates available for unexploited populations, and some of the few existing estimates from exploited populations. My purpose is to identify the apparent range of variability in $M$ within single stocks. The estimates are drawn from references cited by Pauly (1980) and other sources. Only references that reported multiple estimates for $M$ are included, thus excluding most of the references reviewed. Because these estimates are derived from catch data, the stated ranges are "apparent", rather than demonstrably the "true" values.

Estimated rates of natural mortality are not particularly constant for either unexploited or exploited groups, and are only slightly less variable within stocks than they are within species. Although the range of rates within groups may appear relatively small compared to the total range of rates reported for all fish species (e.g., 0.36 to 0.56 for sauger from Lake Nipigon [Table 3] vs. approximately 0.1 to 3.0 for most species listed by Pauly 1980), the maximum and minimum rates reported for single groups differed by at least 50% in 20 of the 22 comparison listed in

Table 3. In at least one case maximum and minimum estimates differ by as much as a factor of 7 (i.e., young vs. old whitefish in Shakespeare Island Lake, Ricker 1947, Table 3).

The range of reported estimates of $M$ for species (rather than single groups or stocks within a species as compared above) is even greater. Even the least variable estimates differed by a factor of 1.75 (75%, male vs. female plaice, Beverton 1964). In whitefish, the species for which the most estimates exist, maximum estimates are **20 times** greater than minimum estimates (Table 3).

TABLE 3.—Ranges in estimates of instantaneous rate of natural mortality in unexploited and exploited fish populations. $M_{max}/M_{min}$ is expressed as the ratio between the maximum ($M_{max}$) and minimum ($M_{min}$) values reported for $M$ for that species, Values in parentheses are total range of estimates and ratios for those species where multiple reports exist.

| Species name | Common name | Body of water | Sex | Age (years) | $M$ range | $M_{max}/M_{min}$ | Source |
|---|---|---|---|---|---|---|---|
| I) Unexploited populations: | | | | | | | |
| *Amboplites rupestris* | rock bass | Nebish Lake | m | 10–12 | 1.47–2.1 | 1.49 | Ricker 1947 |
| | | Nebish Lake | f | 10–14 | 1.1–1.6 | 1.45 | Ricker 1947 |
| | | Nebish Lake | both | 10–14 | 1.08–1.56 | 1.44 | Ricker 1947 |
| | | | | | (1.08–2.1) | (2.01) | |
| *Stizostedion canadensis* | sauger | Lake Nipigon | | 8–14 | 0.36–0.56 | 1.56 | Ricker 1947 |
| *Coregonus clupeaformis* | whitefish | Lake Opeongo | | 6–13 | 0.53 | | Ricker 1947 |
| | | Shakespeare Island Lake | | 11–27 | 0.08–0.60 | 7.51 | Ricker 1947 |
| | | Great Slave Lake | | 17–22 | 0.71–0.99 | 1.39 | Kennedy 1953 |
| | | Lake Nueltin | | 13–15 | 0.84 | | Kennedy 1963 |
| | | Lake McDonald | | 11–14 | 1.34 | | Kennedy 1963 |
| | | | | 9–10 | 1.66 | | Kennedy 1963 |
| | | | | | (0.08–1.66) | (20.75) | |
| *Leucichthys sardinella* | | Ikroavik Lake | | 6–10 | 0.2–1.4 | 7.00 | Wohlschlag 1954 |
| *Cristovomer namayacush* | | Great Slave Lake | | 1–26 | 0.31–1.61 | 5.19 | [1]Kennedy 1954 |
| | | Great Slave Lake | | 15–23 | 0.49–0.92 | 1.88 | [1]Kennedy 1954 |
| | | Great Slave Lake | | 15–23 | 0.52–0.75 | 1.44 | [2]Kennedy 1954 |
| | | | | | (0.31–1.61) | (5.19) | |
| *Perca fluviatilus* | perch | River Thames | m | 3–8 | 0.56–0.98 | 1.75 | Williams 1967 |
| | | River Thames | f | 3–7 | 0.2–0.64 | 3.20 | [3]Williams 1967 |
| | | River Thames | juv | 3–5 | 0.53–1.69 | 3.19 | [3]Williams 1967 |
| | | | | | (0.2–1.69) | (8.45) | |
| *Leuciscus leuciscus* | dace | River Thames | | 5–11 | 0.36–1.31 | 3.64 | [4]Williams 1967 |
| *Alburnus alburnus* | bleak | River Thames | | 3–8 | 0.6–2.4 | 4.00 | [4]Williams 1967 |
| *Rutilus rutilus* | roach | River Thames | | 2–11 | 0.22–1.38 | 6.27 | [4]Williams 1967 |
| | | River Stour | | 3–12 | 0.44 | | Mann 1973 |
| | | | | | (0.22–1.38) | (6.27) | |
| *Cheilodactylus macropterus* | tarakihi | Chatham Islands | | 5–35 | 0.03 | | Vooren 1977 |
| | | Chatham Islands | | 5–22 | 0.08 | | Vooren 1977 |
| | | New Zealand | | | 0.15 | | Vooren 1977 |
| | | | | | (0.03–0.15) | (5.00) | |
| II) Exploited Populations: | | | | | | | |
| *Pleuronectes platessa* | plaice | North Sea | f | 5–13 | 0.08 | | Beverton 1964 |
| | | North Sea | m | 5–13 | 0.14 | | Beverton 1964 |
| | | | | | (0.08–0.14) | (1.75) | |
| *Brevoortia petronus* | gulf menhaden | Gulf of Mexico, Central (1969, 1971) | | 1–3 | 0.7–1.6 | 2.29 | [5]Ahrenholz 1981 |
| | | Gulf of Mexico, Eastern (1969, 1971) | | 1–3 | 0.88–0.98 | 1.11 | [5]Ahrenholz 1981 |
| | | Gulf of Mexico, Western (1969, 1971) | | 1–3 | 1.17–1.23 | 1.05 | [5]Ahrenholz 1981 |
| | | Gulf of Mexico, all areas (1969, 1971) | | 1–3 | 0.95–1.2 | 1.26 | [6]Ahrenholz 1981 |
| | | | | | (0.7–1.6) | (2.29) | |
| *Gadus morhua* | cod | North Sea | | 0.5–1 | 0.59–1.46 | 2.47 | [7]Pope and Knights 1982 |
| *Coregonus clupeaformis* | whitefish | Lake Huron | | 3.8 | 0.34–1.67 | 4.91 | [8]Henderson et al. 1983 |

[1] Increasing with age.

[2] Year to year variation (1946–52); ages 15–23 combined.

[3] Not consistent with age.

[4] Generally increasing with age.

[5] Assuming 20% tag loss rate.

[6] For tag loss rates from 10 to 30%.

[7] 8 different years (1967–75).

[8] 23 different year classes (1947–75).

As discussed previously, these different estimates can lead to at least as great a difference in results produced by fishery analyses such as yield models or stock reconstruction analyses (Section II).

Reported differences in estimates of *M* for whitefish stocks living in Shakespeare Lake compared with other relatively small lakes (e.g., Lake McDonald, Table 3) are particularly significant. Because both stocks are of the same species and living in more or less similar environments (small lakes), one might easily (and incorrectly) assume that both have the same rate of natural mortality; but they did not. The lower rates occurred in the stock occupying a small lake with no predators. This is a clear example of the effect that environment, particularly the predator environment, can have on the realized rate of natural mortality in a fish stock. Obviously, choosing a single appropriate constant for this species would be difficult. Choosing an appropriate species-specific constant for some of the other species with multiple estimates might be difficult as well (e.g., rock bass, lake trout, perch, roach, tarakihi, or menhaden, Table 3).

None of these studies from either unexploited or exploited stocks support the assumption that *M* is constant for any given stock or species, nor are these within-stock ranges particularly narrow. In addition, treatment of the original catch data may have in some cases obscured the "true" variability. Ricker (1947) and Kennedy (1953, 1954, 1963), for example, use a 3-yr smoothing technique to reduce the effects of unequal recruitment; this also serves to reduce variability that may actually be due to differences in natural mortality. Also, single estimates from data collected during only one or two years of sampling (e.g., Wohlschlag 1954; Williams 1967; Mann 1973; Vooren 1977) can be seriously biased by annual changes in either recruitment or mortality rates. If the estimates reported above are even approximately accurate, it is apparent that the range of possible values for *M* is wide, and that variability can be considerable even within single stocks.

A solution to this problem of choosing a reasonable value for *M*, at least for long-lived fish, is suggested by the possibility that **variation** in *M* (not just the mean value) may be related to maximum lifespan. Fish that live for many years must naturally have lower mortality rates than more short-lived fish. These lower rates may also be less variable in the longer lived stocks, if as in many other biological processes, variability is proportional to the mean. This could account for the ubiquity and apparent effectiveness of the constant 0.2 year$^{-1}$, used almost universally for the long-lived (20 to 30 years) and well-studied fish stocks from northern European seas (e.g., Beverton 1964). If so, assuming a constant *M* might be valid for these longer lived stocks.

Unfortunately, the few studies cited above do not support this attractive idea. Although in general, mortality rates decease as lifespan increases, the variability in estimates does not appear to follow the same trend. This may be due partially to the relatively similar lifespans (10 to 20 years) for most of the species for which estimates exist. But the apparent range in rates for the shortest lived species cited above (Ahrenholz 1981, *Brevoortia patronus*, ages 1 to 3 years, *M* range 0.7 to 1.6 year$^{-1}$) is certainly not greater than ranges reported for the longer lived whitefish (Henderson et al. 1983, *Coregonus clupeaformis*, ages 10+ years, *M* range 0.34 to 1.67 year$^{-1}$).

## VI. SUMMARY AND RECOMMENDATIONS

Thus it appears that rates of *M*, or at least rates of *M* derived by existing estimation methods, do in fact vary widely within many fish stocks. Because the variations appear to be considerable and because the results from fishery models can be sensitive to large variations in *M*, one must conclude that assuming constancy without proof can have serious consequences for fishery management.

A better approach may be to discard the notion that a single "best" estimate of *M* can be found, and instead try to tailor estimates of *M* to local groups, based on some combinations of the methods discussed in Section III. Obviously, practical considerations of time and resources will limit the accuracy and precision with which *M* can be estimated. Also, the estimates in the studies reviewed here are prone to all the artifacts mentioned in the previous sections. True rates of natural mortality, and their variability, are still very poorly known for even the great stocks of commercial fish in temperature regions that have been subject to continuous exploitation for decades. Careful, repeated tagging experiments probably hold the most promise for determining with any reasonable degree of accuracy, rates of natural mortality in fish stocks. But even these have inherent problems that are not easily solved. There remains a great need both for new methods, and refinements of the old.

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