The effects of an erroneous natural mortality rate on a simple age-structured stock assessment

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Abstract

The abundance of many stocks is estimated by fitting an age-structured model to catch-at-age and relative abundance data from the commercial fishery and scientific surveys. The natural mortality rate used in the model is usually estimated externally and its value is uncertain. An erroneous natural mortality rate will bias the stock size estimates obtained by fitting the model and it will also bias the yield calculations that are done to choose a harvest rate and recommend quotas. This paper describes the general features of both effects by analyzing a simple age-structured model fitted to artificial data. It is shown that an erroneous natural mortality rate mainly affects the estimates of fishing mortality and hence abundance, but not the estimates of age-specific selectivity. Errors in estimated abundance and target harvest rate are always in the same direction, with the result that, in the short term, extremely high exploitation rates can be recommended (unintentionally) in cases where the natural mortality rate is overestimated and historical exploitation rates in the catch-at-age data are low. A conservative (low) estimate of natural mortality can avoid that danger. Long-term yield under either an F_{MSY} or $F_{35\%}$ strategy is not very sensitive to error in M unless it is grossly underestimated.

Introduction

The last two decades have seen the development of a variety of modern age-structured methods for estimating stock size from a time series of catch-at-age data and some index of relative abundance, most often a scientific survey (Fournier and Archibald 1982; Collie and Sissenwine 1983; Deriso et al. 1985; Methot 1989). A number of them are described and evaluated in a recent study by the National Research Council (1998), where they are called “age-based” or “integrated” methods. All of them are elaborations of the simple DeLury or depletion model (Leslie and Davis 1939; DeLury 1947) in that they infer absolute population size from the effect of known absolute removals on relative abundance. For example, if a brief fishery that removes X tons is observed to reduce relative abundance by 10%, the exploitable stock must have amounted to 10X tons before the fishery started. Modern age-structured methods make the same kind of estimate for every year-class that appears in the catch-at-age data, but in doing so they must account for the effects of natural mortality and age-specific selectivity (survey and/or commercial) on the abundance and catchability of each year-class at each age. Modern methods also allow for process and observation error in the data.

Age-specific selectivity can usually be estimated reasonably well along with other parameters in the course of fitting a model, but not natural mortality. Natural mortality is sometimes estimable in principle (i.e., the correct value can be found if the data are artificial and deterministic), but in practice the estimate is almost always highly variable and unacceptable. Stated another way, the model can usually be fitted equally well with any of a wide range of externally fixed natural mortality rates, meaning that the data do not contain sufficient information to determine the true value. Standard practice is therefore to estimate natural mortality externally and use that estimate as a fixed value when fitting the model. The difficulty is that natural mortality is notoriously difficult to estimate by any means, so the external estimates are not much better than the internal estimates.

Unfortunately the stock size estimates obtained by fitting a model are quite sensitive to the chosen value of natural mortality. The effect of error in the natural mortality rate on stock size estimates obtained by cohort analysis (Pope 1972) has been investigated by a number of authors (Mertz and Myers 1997 and other papers cited therein), but relatively little attention has been given to its effect on stock size estimates obtained by modern assessment methods. The difference presumably results from the nature of the two procedures. Cohort analysis consists of a formula by which historical abundance is back-calculated, so general expressions for the effects of various errors can be derived. Modern assessment methods rely on numerical function minimizers to locate the parameter estimates, so it is not a straightforward task to predict the effect of an error.

Thompson (1994) developed a simple deterministic model in which natural mortality and selectivity were indeterminate and considered the problem of setting a single catch quota when absolute abundance was estimated from a single survey (along with the estimates of survey selectivity). This is somewhat different from the usual age-structured stock assessment, in which absolute abundance is estimated by fitting a model to a time series of relative abundance data. Schnute and Richards (1995) simulated internal estimates of natural mortality along with stock size and other parameters of a conventional stochastic age-structured model fitted to a time series of reliable relative abundance data. Their results confirmed that M is poorly estimated, with the possible exception of cases where the catch-at-age data extend back to the beginning of the fishery. Neither paper considered the effect of error in a fixed external estimate of natural mortality on long-term yield.

The purpose of this paper is to track the effect of an error in natural mortality through the whole assessment cycle, from fitting an age-structured model through choosing a target harvest rate and calculating a recommended quota. The general approach is to derive analytical approximations for the errors induced in the parameter estimates by an erroneous natural mortality rate when a standard age-structured model is fitted to deterministic data. These approximations provide some insight into the behavior of the abundance and selectivity estimates, and they provide a means to work out the effects of a range of errors on the eventual quota recommendation without having to fit the model numerically in each case.

Some of the parameter values and functional forms were chosen to approximate the fishery for Pacific halibut (*Hippoglossus stenolepis)*, but the aim was to develop some general insights into the assessment process in its simplest form rather than to conduct a sensitivity analysis of the actual Pacific halibut assessment. That assessment uses a great deal of fishery and survey data to fit a large age- and length-structured model, and the harvest strategy is designed to meet a number of objectives while allowing for a variety of uncertainties and errors, not including error in the chosen value of natural mortality (Sullivan et al. 1999).

Effect on stock size estimates

The model investigated here is a variant of the classic separable model of fishing mortality first published by Doubleday (1976). In this paper the age-specific selectivity (partial recruitment factor) is treated as a measure of availability rather than relative vulnerability as in the standard version. This modification simplifies some of the algebra and provides nearly the same results. Specifically, let:

$a = 1,\ldots,A$ = age, coded so that the youngest age group in the data has index 1.

$y = 1,\ldots,Y$ = year.

$C_{y,a}$ = catch in number of age *a* fish in year *y*.

$N_{y,a}$ = number of age *a* fish alive at the beginning of year *y*.

F_y = instantaneous rate of fishing mortality in year *y* on fish fully recruited to the fishery.

s_a = commercial fishery selectivity (partial recruitment factor) at age *a*.

$H_{y,a} = s_a \cdot \left(1 - \exp(-F_y)\right)$ = exploitation or harvest rate on age *a* fish in year *y*. In the standard separable model $H_{y,a} = 1 - \exp(-s_a F_y)$.

M = instantaneous rate of natural mortality.

The timing of fishing and natural mortality is not important for this analysis. For simplicity it will be assumed here that the catch is taken during a brief fishery at the beginning of the year so that $C_{y,a} = H_{y,a} N_{y,a} = s_a \cdot (1 - \exp(-F_y)) \cdot N_{y,a}$ and natural mortality follows the fishery so that $N_{y+1,a+1} = N_{y,a} \cdot \left(1 - s_a\left(1 - \exp(-F_y)\right)\right) \cdot \exp(-M)$.

If the catches are generated according to the model and measured without error (or treated that way), the only model parameters are the $\{F_y\}$, $\{s_a\}$, and *M*, and the only data are the catches in the catch-at-age table. Experience has shown that even with *M* fixed externally, this model usually fits the catch-at-age data well but the estimated fishing mortality rates and stock sizes are extremely sensitive to small changes in the catch data, and as a result highly variable. As Doubleday (1976) explained, “This is due largely to the lack of orthogonality between stock sizes and fishing mortalities…. One may increase and the other decrease with little effect on catch.”

To stabilize the estimates, the model is always fitted to one or more series of relative abundance data as well as the catch-at-age data. This serves to locate the correct scale of the stock size estimates by linking the known removals—catches and natural mortality— to the observed changes in relative abundance. Essentially the model becomes an elaboration of the DeLury model, with each year-class in the data providing a series of observations and the parameters being estimated jointly.

More precisely, what the relative abundance data do is to determine the level of total mortality by showing the decline in abundance of individual year-classes. The estimate of fishing mortality is then obtained as the difference between the apparent rate of total mortality and the chosen rate of natural mortality, and finally the stock size estimates are determined by the fishing mortality rates and the catches.

The weak link in this chain is obviously the natural mortality rate, which is usually not known very well. Any error in the chosen value of natural mortality, within limits, will simply be offset by a compensating error in the fishing mortality rates (and stock sizes) so that the correct total mortality is preserved. Thus even when a very good series of relative abundance data is available, it is usually possible to achieve a good fit of the model with a wide range of natural mortality rates, which may imply a wide range of stock sizes.

The ability of the fitted model to closely reproduce the catch-at-age and relative abundance data over a range of natural mortality rates can be exploited to develop analytical approximations for the errors in other parameter estimates induced by an error in the natural mortality rate. This section of the paper does that for fits of the separable model to artificial, error-free catch-at-age and relative abundance data. The results show, at least approximately, what bias in the parameter estimates can be expected on average when the model is fitted to stochastic data.

In some of the cases considered, the fit is very close but not exact, so the deviations have to be weighted to arrive at specific numerical parameter estimates that serve as the standard by which the analytical approximations are judged. For that purpose, a root mean squared relative error (deviation of model prediction from data value, divided by data value) was calculated for both the relative abundance data and the catch-at-age data to obtain an average relative error for each data type. The objective function was the simple sum of the two, so equal weight was given to each data type rather than each data point. Because a close fit was possible in all cases, the weighting of the data types had no practical effect on the fitted estimates.

Consider first the simple case where the full-recruitment fishing mortality rate is the same for all years, so $F_y = F$ throughout, and the relative abundance data are commercial catch per effort in number, a set of values proportional to $s_a N_{y,a}$. Suppose also that the selectivity schedule is asymptotic, so that $s_a = 1$ for two or more of the oldest age groups, and the fitting algorithm forces the estimated selectivities to be asymptotic as well. (For fitting purposes it is essential that at least two of the final selectivities be one. If only the final selectivity is one there is an indeterminacy between the selectivities and total mortality, and the model cannot be fitted.)

Some basic results will be obtained for this simple case and then extended to other cases. Throughout the derivations a circumflex over a symbol will denote the (numerical) estimate of a parameter or derived quantity, e.g. $\hat{F}_y$ will denote the fitted estimate of F_y. Even though not fitted internally, the working value of natural mortality will be denoted $\hat{M}$. The error $(\hat{M} - M)$ will de denoted δ, so $\hat{M} = M + \delta$.

The derivations will rely on two features of the model fits. First it will be assumed that the model can be fitted in the first place, i.e. that the objective function has a unique minimum for each of a range of natural mortality rates and the minimizer locates it. Second it will be assumed that the model fit does in fact reproduce the catch-at-age and relative abundance data closely for each of a range of natural mortality rates. These are the conditions that define the cases of interest in this analysis. Together they imply that if a given set of parameter estimates can be shown to reproduce the data, then by virtue of uniqueness they must be the ones that the minimizer would locate.

Fully recruited age groups

The relative abundance data for fully recruited age groups will reflect the true value of total mortality $Z = F + M$, and the model fit will capture that feature, i.e. $\hat{Z} = Z$. Hence:

$$\hat{F} + \hat{M} = F + M$$
$$\hat{F} + M + \delta = F + M$$
$$\hat{F} = F - \delta$$

So the error in the fitted estimate of full-recruitment fishing mortality will be equal and opposite to the error in the natural mortality rate. Note that if δ is positive, it must be less than F. If it were not, $\hat{M}$ would exceed Z and the model could not be fitted. Similarly if δ is negative it cannot exceed M because $\hat{M}$ is always positive.

Both the model population and the real population must generate the given catch-at-age and relative abundance data. With a constant F, the exploitation rate will be the same for all fully recruited age groups in all years and equal to $H = 1 - \exp(-F)$ for the real population and $\hat{H} = 1 - \exp(-\hat{F}) = 1 - \exp\big(-(F - \delta)\big)$ for the model population. Hence

$$\hat{H} \cdot \hat{N}_{y,a} = H \cdot N_{y,a} = C_{y,a}$$

(1) $$\hat{N}_{y,a} = \big(H / \hat{H}\big) \cdot N_{y,a}$$

These estimates will clearly reproduce the catches exactly and also the relative abundance data (because $\hat{Z} = Z$), so by uniqueness they are the fitted estimates. As a corollary, fully recruited age groups in the real population will also appear as fully recruited in the model population.

Partially recruited age groups

For partially recruited age groups, what the model has to fit is not the true value of total mortality but the ratio of successive relative abundance indexes for each year-class as it passes through the population, that is $\left(s_{y+1,a+1} N_{y+1,a+1}\right) / \left(s_{y,a} N_{y,a}\right)$. Leaving out the year subscript on the understanding that we are dealing with a particular year-class, we can write the required condition on the estimates as:

$$\frac{\hat{s}_{a+1} \hat{N}_{a+1}}{\hat{s}_a \hat{N}_a} = \frac{s_{a+1} N_{a+1}}{s_a N_a}$$

$$\frac{\hat{s}_{a+1}\left[\hat{N}_a\left(1 - \hat{s}_a \hat{H}\right) \cdot \exp\left(-\left(M + \delta\right)\right)\right]}{\hat{s}_a \hat{N}_a} = \frac{s_{a+1}\left[N_a\left(1 - s_a H\right) \cdot \exp\left(-M\right)\right]}{s_a N_a}$$

$$\frac{\hat{s}_{a+1}}{\hat{s}_a} = \frac{s_{a+1}}{s_a} \cdot \frac{\left(1 - s_a H\right)}{\left(1 - \hat{s}_a \hat{H}\right)} \cdot \exp(\delta)$$

(2) $$\frac{\hat{s}_a}{s_a} = \frac{\hat{s}_{a+1}}{s_{a+1}} \cdot \frac{\left(1 - \hat{s}_a \hat{H}\right)}{\left(1 - s_a H\right)} \cdot \exp(-\delta)$$

Let $E_a = \hat{s}_a / s_a$, so $\hat{s}_a = E_a s_a$ and equation (2) can be written as:

$$E_a = E_{a+1} \cdot \frac{\left(1 - E_a s_a \hat{H}\right)}{\left(1 - s_a H\right)} \cdot \exp(-\delta)$$

Solving for E_a gives:

(3) $$E_a = \frac{E_{a+1}}{\left(1 - s_a H\right) \cdot \exp(\delta) + E_{a+1} s_a \hat{H}}$$

Because the selectivities are asymptotic, $\hat{s}_A = s_A = E_A = 1$ and the fitted selectivities $\{\hat{s}_a = E_a s_a\}$ can be calculated recursively with equation (3).

Values of the selectivities calculated in this way will match the relative abundance data, meaning the relative magnitudes of the index for successive age groups. The oldest age group must be fully recruited $(s_A = \hat{s}_A = 1)$, so the estimates of numbers at age corresponding to the selectivities must satisfy the following relationship at all ages:

$$\frac{\hat{s}_a \hat{N}_a}{\hat{N}_A} = \frac{s_a N_a}{N_A}$$

$$\hat{N}_a = \frac{s_a}{\hat{s}_a} \cdot \frac{\hat{N}_A}{N_A} \cdot N_a$$

$$\hat{N}_a = \frac{s_a}{\hat{s}_a} \cdot \frac{H}{\hat{H}} \cdot N_a \qquad (4)$$

The corresponding calculated catch is:

$$\begin{aligned} \hat{C}_a &= \hat{H}_a \hat{N}_a \\ &= \left(\hat{s}_a \hat{H}\right) \cdot \left(\frac{s_a}{\hat{s}_a} \cdot \frac{H}{\hat{H}} \cdot N_a\right) \\ &= s_a H N_a \\ &= C_a \end{aligned}$$

Even with an error in $\hat{M}$, therefore, the fitted model can reproduce the catch-at-age and relative abundance data exactly. Like Thompson's (1994) model, this form of the simple age-structured model is a case where the natural mortality rate and the selectivity (i.e., availability) parameters are formally indeterminate. This means that even with perfect data, M cannot be estimated internally and fitting the model requires an external estimate.

General features of the biased fits

Some examples will illustrate the effect of error in the chosen value of natural mortality on model fits. Deterministic catch-at-age and relative abundance data for these examples were generated using the availability form of the separable model described above. True selectivity at age was calculated with a function that has the form of the left limb of a normal density and whose two parameters are the age at full recruitment (a_f = coded age 9) and the age at half recruitment (a_h = coded age 4):

$$s_a = \exp\left\{-(\log 2) \cdot \left(a_f - a\right)^2 \Big/ \left(a_f - a_h\right)^2\right\} \text{ for } a < a_f \text{ and } s_a = 1 \text{ for } a \geq a_f$$

While the true age-specific selectivities were calculated with this parametric function, they were estimated as individual parameters when the model was fitted, and the last three (out of 15) were fixed at one. Parameter estimates obtained by fitting the model numerically were compared with the values obtained with the computing formulas derived above. The agreement was exact in every case.

Table 1 shows the fitted estimates for a range of true natural mortality rates from 0.10 to 0.30 when fishing mortality F is 0.15 and the model is fitted with the widely popular estimate $\hat{M} = 0.20$. For example, for true M = 0.10 (Case 1), the error in $\hat{M}$ is $\delta = \hat{M} - M$ = +0.10. When the model is fitted, the full-recruitment fishing mortality rate is estimated to be $\hat{F} = F - \delta$ =0.05, and the abundance of fish in the fully recruited age groups is estimated to be $\left(H/\hat{H}\right) =$ 2.86 times the true abundance, a sizable error. The estimate of (coded) age 1 abundance is even further off, 4.01 times the true abundance, because for partially recruited fish the effect of the underestimate of fishing mortality is compounded by the underestimate of selectivity. An underestimate of natural mortality by the same amount ($\delta = -0.10$, Case 5) produces an underestimate of abundance by about 40% (the factor 0.63). For an error of a given magnitude $|\delta|$ in the natural mortality rate, the relative error in the abundance estimates is much larger in the case of an overestimate than an underestimate

The reasons for this behavior are apparent from the formula for the relative error:

$$
\begin{aligned}
\frac{\hat{N} - N}{N} &= \frac{\left(H/\hat{H}\right)\cdot N - N}{N} \\
&= \frac{\left(1 - \exp(-F)\right)}{\left(1 - \exp(-(F - \delta))\right)} - 1 \\
&\approx \frac{\delta}{(F - \delta)} \text{ for small } F - \delta > 0
\end{aligned}
$$

Obviously a large F will swamp even a large δ, but even a small δ can result in a sizable error when F is small, and more so if δ is positive. The worst case is a positive δ only a little smaller than F. In this case stock size is severely overestimated, although as explained below the behavior of the estimates changes slightly as $\left(F - \delta\right)$ goes to zero so that the outcome is not quite as bad as the formula above suggests. Note that the true value of M has no effect on the error.

The selectivity estimates are much less sensitive to error in the natural mortality rate (Figure 1). In terms of the estimated age at 50% recruitment (determined by fitting the parametric function to the individual selectivity estimates in each case), the corresponding variation is at most 10%. In relative terms the error is larger for the younger age groups, and that has a significant effect on estimation of the stock-recruitment relationship (discussed below), but even for partially recruited age groups the location of the selectivity curve is defined quite well even when the natural mortality rate is way off, and for age groups that are estimated to be more than 50% recruited there is hardly any error.

The selectivity estimates are resistant to error in the natural mortality rate simply because only a small adjustment to the true values is needed to fit the data. Rewriting equation (2) with $H = 1 - \exp\left(-F\right)$ and $\hat{H} = 1 - \exp\left(-\left(F - \delta\right)\right)$ gives:

$$\left(\frac{\hat{s}_a}{s_a}\right) = \left(\frac{\hat{s}_{a+1}}{s_{a+1}}\right) \cdot \frac{\left(1 - \hat{s}_a\left(1 - \exp\left(-\left(F - \delta\right)\right)\right)\right)}{\left(1 - s_a\left(1 - \exp(-F)\right)\right) \cdot \exp(\delta)}$$

$$\approx \left(\frac{\hat{s}_{a+1}}{s_{a+1}}\right) \cdot \frac{\exp\left(-\hat{s}_a\left(F - \delta\right)\right)}{\exp\left(-s_a F\right) \cdot \exp(\delta)}$$

$$\approx \left(\frac{\hat{s}_{a+1}}{s_{a+1}}\right) \cdot \exp\left(-\delta\left(1 - s_a\right)\right)$$

Again by virtue of the asymptotic selectivities $\left(\hat{s}_A / s_A\right) = 1$ so

$$\left(\frac{\hat{s}_a}{s_a}\right) \approx \prod_{i=a}^{A-1} \exp\left(-\delta\left(1 - s_i\right)\right) = \exp\left(-\delta \sum_{i=a}^{A-1}\left(1 - s_i\right)\right)$$

For an age group that is 50% recruited, $\left(1 - s_i\right)$ will be 0.5 and because selectivity is normally increasing rapidly at this point the remaining terms in the summation will sum to perhaps another 0.5, for a total of around 1. The ratio $\left(\hat{s}_a / s_a\right)$ will therefore be on the order of $\exp\left(-\delta\right) \approx 1 - \delta$ and the relative error in $\hat{s}_a$ will be on the order of δ, which cannot be much more than 10%. For the smaller selectivities the relative error will be larger, but the absolute error will still be modest, as in the examples shown. Note that here, too, the size of the error does not depend on the true value of M.

Variable fishing mortality

All of the analytical results derived thus far have relied on the fishing mortality rate F remaining constant from year to year and therefore from age to age (for fully recruited age groups), but they also hold approximately when the $\{ F_y \}$ are allowed to vary, so long as there is no strong trend or contrast in the series and the error $\delta = \hat{M} - M$ is not too large relative to the mean of the $\{ F_y \}$. In this situation, if $\overline{F}$ is the mean of the true values $\{ F_y \}$, the mean of the estimates $\{ \hat{F}_y \}$ is $\hat{\overline{F}} \approx \overline{F} - \delta$, and the annual estimates of harvest rates are:

$$\hat{H}_y \approx H_y \cdot \left(\frac{\hat{\overline{H}}}{\overline{H}}\right) = H_y \cdot \left(\frac{1 - \exp(-\overline{F})}{1 - \exp\left(-(\overline{F} - \delta)\right)}\right)$$

For fully recruited fish the estimated numbers at age are $\hat{N}_{y,a} \approx \left(\frac{\overline{H}}{\hat{\overline{H}}}\right) \cdot N_{y,a}$, as in the case of constant fishing mortality, and because equation (2) is not at all sensitive to F, equations (3) and (4) also hold (to a close approximation) for partially recruited age groups when the estimated selectivities are calculated analytically with $\overline{F}$ in place of a constant F.

The correspondence is close but not exact because when there is error in $\hat{M}$ and variance in the $\{F_y\}$, the analytical approximations do not track the $\{Z_y\}$ exactly, and the minimizer redistributes the total fishing mortality slightly so that the fitted $\{\hat{Z}_y\}$ will track better. That is easy to do when δ is negative because then $\hat{\bar{F}} > \bar{F}$ and the $\{\hat{Z}_y\}$ tend to overshoot the $\{Z_y\}$. Redistributing a small amount of fishing mortality requires only a small relative change in any of the $\{\hat{F}_y\}$, so they can be made to both track the $\{Z_y\}$ and produce the catches very closely—to within a few percent.

When δ is positive, and particularly when $(\bar{F} - \delta)$ is near zero, the problem is harder and the best solution is to create a small amount of fishing mortality over and above $(\bar{F} - \delta)$, even at the cost of exceeding $\bar{Z}$ slightly. As a purely empirical finding in the specific case of the model studied here, when the $\{F_y\}$ were drawn from a uniform distribution running from $0.5\bar{F}$ to $1.5\bar{F}$ and δ was positive, the fitted mean fishing mortality rate was approximately $\hat{\bar{F}} \approx (\bar{F} - \delta) + 0.05\delta = \bar{F} - 0.95\delta$. So for example with $\bar{F} = 0.15$ and $\delta = +0.10$, the estimate averaged $\hat{\bar{F}} = 0.055$ instead of 0.050 as in the case of constant *F*. This is a small absolute difference, but it can have a significant effect on the estimates of abundance because they are inversely proportional to $\hat{\bar{H}}$. In this example the estimated abundance of fully recruited fish is 2.86 times the true value when *F* is constant (Table 1), but on average only 2.60 times when the $\{F_y\}$ vary in the manner stated.

This behavior is demonstrated in Figure 2, which shows the results of 1000 simulations. For each trial, a true mean fishing mortality $\bar{F}$ was chosen from a uniform $[0,0.5]$ distribution, a true natural mortality *M* was drawn from a uniform $[0,0.3]$ distribution, and a working value $\hat{M}$ was drawn from a uniform $[0, \min(0.3, \bar{F} + M)]$ distribution. Thus for $\bar{Z} < 0.3$, $\hat{M}$ was drawn from a uniform $[0, \bar{Z}]$ distribution (the feasible range), and for $\bar{Z} \geq 0.3$ from a $[0,0.3]$ distribution. Catches at age were generated with annual fishing mortality rates drawn from a uniform $[0.5\bar{F}, 1.5\bar{F}]$ distribution, and the model was fitted numerically to the artificial data. For negative values of δ, the regression line is $(\hat{\bar{F}} - \bar{F}) = -1.00 \cdot (\hat{M} - M) = -\delta$ so $\hat{\bar{F}} = \bar{F} - \delta$ as in the case of constant fishing mortality. For positive values of δ, the regression line has slope –0.95, so $\hat{\bar{F}} = \bar{F} - 0.95\,\delta$. Note that the variability of the fitted estimates increases as $|\delta|$ increases.

A related peculiarity of the fits obtained when $(\bar{F} - \delta)$ is near zero and the $\{F_y\}$ vary is that the selectivities of the older age groups, including some fully recruited ones, are made to sag so as to offset the excess of $\hat{\bar{Z}}$ over $\bar{Z}$ (Figure 3). This is an exception to the general rule that the selectivity of older fish is well estimated even when the natural mortality rate is in error.

With the adjustment $\hat{\bar{F}} = \bar{F} - 0.95\delta$ for $\delta > 0$ (and the approximate selectivities calculated with that value), the analytical approximations do a good job of predicting the numerically fitted estimates when fishing mortality varies. Specifically, let $K_f = \hat{\bar{N}}_f / \bar{N}_f$, the ratio of the fitted estimate of average abundance of fully recruited age groups to the true value, and let $K_1 = \hat{\bar{N}}_1 / \bar{N}_1$ denote the same ratio for the recruits (coded age group 1). As shown in Figure 4, the analytical approximations predict the actual fitted estimates quite well across the large range of errors contained in the 1000 simulated cases. The scatter increases with the error, but only becomes substantial when the fitted estimates exceed the true values by an order of magnitude.

Trends in fishing mortality

When the true fishing mortality rates contain a major trend, or a contrast between periods, and the natural mortality rate is wrong, the model fits to deterministic data always show large residuals with very clear trends. A good fit is simply impossible. This suggests that in principle the natural mortality rate should be estimable in these cases, but in practice other sources of variance tend to obscure the patterns resulting from lack of fit. At any rate these cases are beyond the scope of this paper, which is concerned with situations where many good fits are possible.

Effect on yield calculations and harvest rates

Many stocks are managed by applying a target harvest rate to estimated present stock size to arrive at a recommended upper limit for the quota. The target harvest rate is based either on an estimate of the spawner-recruit relationship (F_{MSY}) or on a target value of spawning biomass per recruit, typically 35% or 40% of the unfished value ($F_{35\%}$ or $F_{40\%}$; Clark 1991). Error in the working value of natural mortality affects these calculations in three ways:

1. *Biased estimate of spawner productivity*. For a given set of life history parameters, the optimum harvest rate for a stock depends mostly on the slope of the spawner-recruit relationship at the origin, which is the productivity of spawners at very low stock levels. In most stocks the bulk of spawners are fully recruited and the recruits are the youngest age group in the model (coded age 1). In this situation an error in the natural mortality rate will lead to an estimate of the slope equal to the true value multiplied by:

$$\frac{\left(\hat{N}_1/\hat{N}_f\right)}{\left(N_1/N_f\right)} = \frac{\left(\hat{N}_1/N_1\right)}{\left(\hat{N}_f/N_f\right)}$$
$$= \left(K_1/K_f\right)$$
$$= \left(s_1/\hat{s}_1\right)$$

(by equation 4). For example an overestimate of natural mortality lowers the estimated selectivities of partially recruited age groups and elevates the estimated numbers, resulting in an overestimate of the slope parameter of the spawner-recruit relationship. With constant $F = 0.15$, $M = 0.10$, and $\hat{M} = 0.20$, the multiplier is $4.01/2.86 = 1.40$ (Table 1). With variable fishing mortality it is $3.77/2.60 = 1.45$, about the same.

2. *Biased estimate of recruit productivity.* Other things being equal, yield and spawning biomass per recruit decrease as the natural mortality rate increases. In the case of yield calculations based on an estimated spawner-recruit relationship, an overestimate of natural mortality will result in an underestimate of recruit productivity, which to some extent should offset the associated overestimate of spawner productivity. When a reference fishing mortality rate like $F_{35\%}$ is calculated, an error in natural mortality will affect both the unfished and fished values of spawning biomass per recruit, but in practice $F_{35\%}$ is usually quite sensitive to the natural mortality rate. Both target rates will also be affected by the distorted selectivities, but not very much.

3. *Translation from a target harvest rate to a real harvest rate.* A catch quota recommendation is calculated by applying the target harvest rate to the numbers in the model population, but then the catch is taken from the real population where the numbers are different, so the real harvest rate is different. Let $\hat{H}^*$ denote the estimated target (full-recruitment) harvest rate, C^* the recommended quota, and $\tilde{H}_1$ the resulting real harvest rate in the first year. Then for fully recruited fish

$$C_f^* = \hat{H}^* \hat{N}_f = \hat{H}^* \left(H/\hat{H} \right) N_f \quad \text{so} \quad \tilde{H}_1 = \hat{H}^* \left(H/\hat{H} \right)$$

When $\hat{M}$ is an overestimate, $\hat{H}$ is an underestimate, so an overestimate of natural mortality will generally result in a real harvest rate higher than the target. In cases where H is low, $H/\hat{H} \approx F/(F - \delta)$ and even a small overestimate can cause a large overshoot.

If $\hat{H} = \hat{H}^*$, then $\tilde{H}_1 = H$ and the fishery will continue indefinitely at a harvest rate of $\tilde{H}_1$. That is, the equilibrium harvest rate for a given nominal target fishing mortality rate F^* (e.g., F_{MSY} or $F_{35\%}$) and a given natural mortality estimate $\hat{M}$, is the one for which the estimate of average fishing mortality in the catch-at-age data $\hat{F}$ is equal to the estimate of the nominal target rate $\hat{F}^*$. And since $\hat{F} = F - \delta$, the real equilibrium rate $\tilde{F}_{eq}$ is:

(5) $$\tilde{F}_{eq} = \hat{F}^* + \delta$$

This is a stable equilibrium, because $\tilde{H}_1$ will be greater than H when $\hat{H} < \hat{H}^*$ and it will be less than H when $\hat{H} > \hat{H}^*$. If natural mortality is severely underestimated, $\tilde{F}_{eq}$ can be negative, meaning that estimated fishing mortality $\hat{F}$ exceeds $\hat{F}^*$ even when real fishing mortality is nil, so there is no equilibrium.

Calculated effects for a specific case

The consequences of error in the natural mortality rate were calculated for a specific life history similar to Pacific halibut, using the analytical approximations derived above for the case of variable fishing mortality. The advantages of using the approximations are that they save a great deal of time, they show the average behavior of the fitted estimates (averaged over the variability induced by different sequences of fishing mortality rates), and they avoid the computational problems that can occasionally arise during attempts to fit the model numerically, even to artificial data.

The life history parameters used in the calculations are shown in Table 2. They correspond roughly to a longline fishery for Pacific halibut with no minimum size limit. The age-specific selectivities are the ones described above. The oldest age group in the computations is not a pooled age group; older fish are simply disregarded because of uncertainty about growth and mortality at those ages.

Recruitment levels for yield calculations were based on a Beverton-Holt spawner-recruit relationship:

$$R = \alpha S \big/ \left(1 + \beta S\right)$$

where *R* is recruitment in number at coded age 1 and *S* is parent spawning biomass. For a given fishing mortality rate *F* and resulting spawning biomass per recruit $\mathrm{spr}\left(F\right)$, the equilibrium spawning biomass for this relationship is $\left(\alpha \cdot \mathrm{spr}(F) - 1\right) \big/ \beta$. The slope at the origin α was set to 0.12 recruits per unit of spawning biomass, a value for which $F_{MSY} = F_{35\%} = 0.23$ for $M = 0.20$. The scale parameter β has no effect other than to scale all the calculated yields.

For the life history parameters and spawner-recruit relationship used here, the true values of F_{MSY} and $F_{35\%}$ depend on the true value of *M* as follows:

M	0.05	0.10	0.15	0.20	0.25	0.30
F_{MSY}	0.17	0.21	0.23	0.23	0.21	0.18
$F_{35\%}$	0.14	0.16	0.19	0.23	0.29	0.36

Evidently F_{MSY} is much less sensitive to the true natural mortality rate than is $F_{35\%}$ in this case. Figure 5 shows how the true value of F_{MSY} varies when the slope of the spawner-recruit relationship is varied by a factor of four above and below the central value. At the lower end of the spawner productivity range, the true value of F_{MSY} is more sensitive to the slope parameter than to *M*, while at the upper end it is more sensitive to *M* than to the slope parameter. Within a factor of two of the central value, the slope parameter is much more important than the value of

M. The true value of $F_{35\%}$ is not affected by the slope of the spawner-recruit relationship; contours of $F_{35\%}$ analogous to the ones in Fig. 5 would be vertical lines.

Short-term effects

The error in estimated stock size depends on the average level of fishing mortality in the catch-at-age data and on the error in natural mortality, but not on the true value of natural mortality. These errors were computed over a grid of average fishing mortality rates $0 \le \overline{F} \le 0.5$, true natural mortality rates $0 < M \le 0.3$, and estimated natural mortality rates $0 < \hat{M} \le \min(0.3, \overline{F} + M)$. Even at the higher levels of $\overline{F}$, and even when the error in $\hat{M}$ is 0.10 or less, there are substantial errors in the biomass estimates (Fig. 6), but they are generally less than 25% when $\overline{F} \ge 0.3$. At lower levels of $\overline{F}$ even small errors in $\hat{M}$ result in large errors, e.g. a two- or threefold overestimate when $\overline{F} = 0.1$ and $\hat{M} = M + 0.05$.

The errors in estimates of F_{MSY} and $F_{35\%}$ depend on the true value of natural mortality and the error in estimated natural mortality, but not (significantly) on the average level of fishing mortality in the catch-at-age data. Overestimates of *M* result in overestimates of the target rates (Fig. 7a and b). Estimates of F_{MSY} are somewhat less sensitive to error in the estimate of natural mortality than are estimates of $F_{35\%}$. For example, with true $M = 0.20$, the estimate $\hat{F}_{MSY}$ varies from about 0.18 to 0.27 for values of $\hat{M}$ within ± 0.10 of the true value, while the estimate $\hat{F}_{35\%}$ varies from about 0.15 to 0.40. In fact the estimates $\hat{F}_{MSY}$ are quite serviceable whenever the error in $\hat{M}$ is less than 0.10.

Error in the estimate of the target harvest rate compounds the error in the stock size estimate, with the result that real harvest rates differ from the nominal targets by even more than the stock size estimates differ from the true values (Fig. 8a and b). In particular, the real short-term harvest rate under either an F_{MSY} or $F_{35\%}$ strategy can easily be two or three times the desired value when the average fishing mortality rate in the catch-at-age data is low and the natural mortality rate is overestimated by as little as 0.05. Underestimates of natural mortality result in much smaller errors, so in the short term it is preferable to adopt a conservative (i.e., low) estimate of natural mortality if the average fishing mortality rate is low, or may be low.

Equilibrium conditions

Under either harvest strategy, the real harvest rate will tend toward the equilibrium given by equation (5). This limits the range of potential errors, but even at equilibrium the real harvest rate under either strategy can range from about a quarter to twice the desired value for errors of 0.10 or less in the estimate of natural mortality (Figs. 9a and 9b). The F_{MSY} strategy is somewhat better behaved across the whole range of true natural mortality rates and errors than the $F_{35\%}$ strategy.

In terms of yield, both strategies perform quite well for errors up to ± 0.10 in the natural mortality rate, with F_{MSY} again more consistent across the whole range considered (Figs. 10a and b). The only region of somewhat poor performance is where the true natural mortality is low (less than 0.20) and it is substantially underestimated. But the region of good performance is quite wide, so a conservative (low) estimate of natural mortality will still perform well so long as it is not overly conservative.

Like the actual yield, the estimate of MSY is close to the true value for errors up to ± 0.10 in the natural mortality rate (Fig. 11). Depending on the value used, the impression may be of a smaller, more productive stock or a larger, less productive stock, but the potential long-term surplus production comes out about the same. The robustness of the MSY estimate only holds in the vicinity of the equilibrium fishing mortality rate; MSY calculations based on estimates at much higher or lower fishing mortality rates can differ greatly from the correct value, in either direction.

Other model formulations

All of the analysis above refers to the availability version of the separable model of fishing mortality fitted to commercial catch per effort. In fact the vulnerability version of the separable model is more common, and it is almost always fitted to a survey index of abundance. In many fisheries the separable model of fishing mortality cannot be used at all because commercial selectivity is known or suspected to be variable. This section will extend the analysis to cover those cases.

Standard separable model

If age-specific selectivity is treated as relative vulnerability rather than availability, age-specific harvest rates for a brief fishery are calculated as $H_a = 1 - \exp(-s_a F)$ and commercial catch per effort is a set of values proportional to { $H_a N_a$ } rather than { $s_a N_a$ }. The selectivities { $\hat{s}_a$ } that will reproduce the relative abundance data in this case when fishing mortality is constant and $\hat{M} \neq M$ can be calculated with computing formulas analogous to equations (2) and (3), and it can be shown that these selectivities and the corresponding estimated numbers at age will also generate the catch-at-age data exactly. The same result can be obtained when the Baranov catch equation is used. The form of the catch equation will not affect the general features and conclusions of the analysis performed with the availability version of the model, so they apply to these cases.

While it is possible to choose a catch equation and relative abundance index that will result in exact agreement between the model predictions and the data even when $\hat{M}$ is in error, inconsistencies are also possible. For example, if the standard separable model is used to generate the catches but the index of abundance is the one used above (proportional to $s_a N_a$), it is not possible to reproduce both data sets exactly when there is an error in the natural mortality rate. The relative abundance data and the catch-at-age data require slightly different selectivities, and the fitted selectivities are a compromise. They are a very good compromise in that the model fit is still good to several digits, but it is not exact.

Survey index of abundance

Suppose that fishing mortality is constant and the separable model has been fitted exactly to commercial catch per effort as above, the index being proportional to $s_a N_a$. Now a survey index with different selectivities, say $t_a N_a$, is brought into the fit. By equation (4),

$$t_a N_a = t_a \cdot \left(\frac{\hat{s}_a}{s_a}\right) \cdot \left(\frac{\hat{H}}{H}\right) \cdot \hat{N}_a = \hat{t}_a \hat{N}_a$$

so with (normalized) survey selectivities { $\hat{t}_a$ } the existing fit will reproduce the survey index exactly and therefore those are the fitted survey selectivities, even if commercial catch per effort is left out of the fit.

Note that after normalization $\left(\hat{t}_a / t_a\right) = \left(\hat{s}_a / s_a\right)$, so an error in natural mortality will alter the survey selectivities proportionally just the same as the commercial selectivities and affect the stock size estimates and yield calculations in exactly the same way, so all of the analysis carries over to this case.

Note also that when there is an error in $\hat{M}$, the estimated age-specific survey selectivities { $\hat{t}_a$ } that are required to reproduce the data depend on the age-specific commercial selectivities and the level of fishing mortality. If the estimated survey selectivities are viewed as a solution to the problem of reconciling the data with the wrong value of $\hat{M}$, then the solution is only good for a specific set of age-specific commercial selectivities and a specific harvest rate.

Non-separable models

In cases where the separable model of fishing mortality is not used, the catch-at-age estimates are treated as known removals and year-class sizes are estimated directly along with the selectivities of the survey index to which the model is fitted. In fits to deterministic data where the separable model is correct and an exact (or at least very close) fit is possible for a range of natural mortality rates, this procedure will necessarily produce the same estimates as the separable model, so to this extent the results of the present analysis carry over.

If the separable model is not correct, and the natural mortality rate is wrong, a good fit of the non-separable model to deterministic data will not be possible. There will be large, systematic errors in the predicted survey index, similar to the bad fits of the (correct) separable model to data containing a strong trend or contrast in fishing mortality. This is because, as explained above, the estimated survey selectivities that reconcile the data and an incorrect value of $\hat{M}$ are only good for a single set of commercial selectivities and a single level of fishing mortality.

As a concrete example, consider the simple case of a data set where the first half of the catch-at-age data is generated by a separable model with a gradually increasing commercial selectivity like the one used above, and the second half is generated by a knife-edge model. Either half could be fitted exactly by the separable model with a range of natural mortality rates, but the estimated survey selectivities would be different for the two halves in every case except the one where the correct natural mortality rate was used. Fits of the non-separable model to the two halves would produce the same results, and fits of either model to the entire data set would produce a compromise estimate of survey selectivities with large residuals in the predicted survey index.

As explained above, good fits of the separable model are possible for a range of natural mortality rates even when fishing mortality is variable so long as there is no marked trend or contrast, and the same is presumably true for commercial selectivity. That is, good fits of an age-structured model (separable or non-separable) could presumably be achieved with a range of natural mortality rates even if commercial selectivity varies from year to year, so long as there is no marked trend or contrast in the time series. Where that is the case, the results obtained above should apply even when a non-separable model is fitted.

Discussion

This paper has attempted to work out the effects of an erroneous natural mortality rate on each step of a simple stock assessment in order to find out what the eventual consequences are for the stock and to see whether there is any good strategy for dealing with uncertainty in the natural mortality rate, which is present in almost every assessment. A number of conclusions have emerged. Strictly speaking these conclusions apply only to cases where the separable model is correct and there is not a strong trend in (true) fishing mortality, but as a practical matter they should hold approximately in any case where an equally good fit can be obtained with a range of natural mortality rates.

Choosing a good external estimate of natural mortality

The results show that if the average (true) fishing mortality rate in the catch-at-age data is high enough (say 0.3 or greater), error in the natural mortality rate up to ±0.10 is not a serious concern. The working value can be carried through all the calculations and the recommended yields will be reasonable even though the stock size and harvest rate estimates may be poor.

If the average fishing mortality rate in the historical data is low, a modest overestimate of the natural mortality rate can produce large errors in stock size estimates, and the corresponding quota recommendations will represent very high real harvest rates in the short term. Underestimates of the natural mortality rate carry little penalty in terms of long-term yield and result in recommended real harvest rates lower than the nominal target. For management purposes, therefore, it makes sense to use a conservative (low) estimate rather than a point estimate of natural mortality as the working value when fishing mortality is low, or may be low. Nor is there any yield penalty in using a conservative estimate when fishing mortality is substantial, so this seems to be a sensible policy in general. The only hazard to avoid is a gross underestimate of natural mortality, which in the long term can result in a large underestimate of fishing mortality, a large overestimate of actual fishing mortality, and a very low real harvest rate (far below target).

A low estimate of natural mortality also has some computational advantages in that numerical model fits can produce strange results (or no results) when the working value of natural mortality is near the level of total mortality *Z* indicated by the relative abundance data. To avoid that, one can use a very low working value $\hat{M}$ to fit the model initially. That will provide a reliable estimate of total mortality and of the selectivity of age groups that are mostly or fully recruited. The total mortality estimate will then provide a useful upper limit for any higher value of $\hat{M}$ that might be considered as a routine working value.

Modeling and estimating selectivities

The selectivities of age groups that are mostly or fully recruited are quite well determined by the data even when $\hat{M}$ is wrong, so long as it not too close to *Z*. This means that it should always be possible to fit them individually rather than using a parametric function, and their behavior can be useful diagnostic of a poor choice of $\hat{M}$. Moreover, while the use of a parametric function can provide a modest variance reduction if it is correctly specified, it can also result in large errors if it is incorrectly specified (Kimura 1990), or, more subtly, even if it is correctly specified but $\hat{M}$ is wrong.

Choosing a target harvest rate

Yield calculations done to choose a target harvest rate are affected by an error in $\hat{M}$ in several ways. For the case considered here, the estimate of F_{MSY} was less sensitive to both the true and the working values of natural mortality than was $F_{35\%}$. This is a good reason to attempt to use available spawner-recruit data to choose a harvest rate if there are enough points at low stock sizes to provide a meaningful estimate of the slope parameter. In terms of long-term yield, the estimated F_{MSY} and $F_{35\%}$ harvest rates both performed well when there was an error in $\hat{M}$.

Estimating *M* internally

It has been conjectured (e.g. Thompson 1994 and citations therein) that the rate of natural mortality can be estimated internally so long as the selectivities are asymptotic. This paper has shown that for some common models with asymptotic selectivities, the conjecture is false when fishing mortality is not highly variable and the selectivities are estimated individually.

On the other hand, if it is the parameters of a selectivity function that are estimated (rather than individual selectivities), it is possible to estimate *M* internally with the model studied here even when fishing mortality is constant, and with deterministic data the estimate is of course correct if the function is correctly specified. Sets of individually estimated selectivities can be located that reproduce the data exactly for any value of $\hat{M}$, and they are all very similar in shape, but only for the true value do the selectivities have *exactly* the shape required by the function.

The resulting estimate of *M* is clearly artificial because it relies entirely on the precise shape of the specified selectivity function rather than on any information in the data. In practice the form of the selectivity function is specified arbitrarily, and it is certainly not precisely the right one.

Simulation exercises in which stochastic data are generated with a given selectivity function and then *M* is estimated internally using knowledge of the form of the function (e.g. Schnute and Richards 1995) do not provide a real test of the performance or even the feasibility of internal estimates of *M* in real assessments. This side effect of using a parametric selectivity function (i.e., making *M* appear to be estimable when in fact it is not) is another reason to prefer individual selectivities.

In principle the rate of natural mortality can be estimated from deterministic data given sufficient contrast in fishing mortality and/or selectivity, but in practice real data usually contain too much noise and too little contrast for that. Given good fishing effort data $\{ f_y \}$ and good estimates of total mortality, it should be possible to estimate *M* by decomposing $Z_y = q \cdot f_y + M$ in the course of fitting the model, but even with some of the world's best data of both kinds it was not possible to estimate the natural mortality rate of Pacific halibut by this method (McCaughran and Deriso 1988).

While estimating *M* internally may not be practical in many cases, experimenting with different working values should be considered as a possible way to explain or eliminate systematic trends in the residuals, particularly around the index of relative abundance. If nothing else the exercise will provide a broader view of the model fit than simply focusing on the results obtained with a single, essentially arbitrary working value.

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Table 1. True parameter values and fitted estimates for a range of true natural mortality rates M when fishing mortality is constant at F = 0.15 and the model is fitted with $\hat{M}$ =0.20. The true selectivities at age are listed under Case 3.

Quantity	Case 1	Case 2	Case 3	Case 4	Case 5
True natural mortality rate M	0.10	0.15	0.20	0.25	0.30
Chosen natural mortality rate $\hat{M}$	0.20	0.20	0.20	0.20	0.20
Error $\delta = \hat{M} - M$	+0.10	+0.05	0.00	-0.05	-0.10
True fishing mortality rate F	0.15	0.15	0.15	0.15	0.15
Estimated fishing mortality rate $\hat{F}$	0.05	0.10	0.15	0.20	0.25
Estimated selectivity at (coded) age: 1	0.12	0.14	0.17	0.20	0.23
2	0.20	0.23	0.26	0.29	0.32
3	0.31	0.34	0.37	0.40	0.43
4	0.44	0.47	0.50	0.53	0.55
5	0.60	0.62	0.64	0.66	0.68
6	0.75	0.77	0.78	0.79	0.80
7	0.88	0.89	0.90	0.90	0.91
8	0.97	0.97	0.97	0.97	0.98
9+	1.00	1.00	1.00	1.00	1.00
Estimated age at 50% recruitment	4.38	4.20	4.00	3.79	3.57
Estimated age at 100% recruitment	8.92	8.96	9.00	9.05	9.10
Estimated age 9+ abundance as a multiple of true numbers	2.86	1.46	1.00	0.77	0.63
Estimated age 1 abundance as a multiple of true numbers	4.01	1.72	1.00	0.66	0.47

Table 2. Age-specific parameters used in yield calculations.

Age	Coded age	Selectivity	Mean weight	Maturity
6	1	0.17	16.83	0.03
7	2	0.26	16.83	0.06
8	3	0.37	16.83	0.12
9	4	0.50	20.65	0.21
10	5	0.64	23.36	0.34
11	6	0.78	26.07	0.50
12	7	0.90	28.78	0.68
13	8	0.97	31.49	0.84
14	9	1.00	34.20	0.96
15	10	1.00	36.92	1.00
16	11	1.00	39.63	1.00
17	12	1.00	42.34	1.00
18	13	1.00	45.05	1.00
19	14	1.00	47.76	1.00
20	15	1.00	50.47	1.00
21	16	1.00	53.18	1.00
22	17	1.00	55.89	1.00
23	18	1.00	58.60	1.00
24	19	1.00	61.31	1.00
25	20	1.00	64.02	1.00

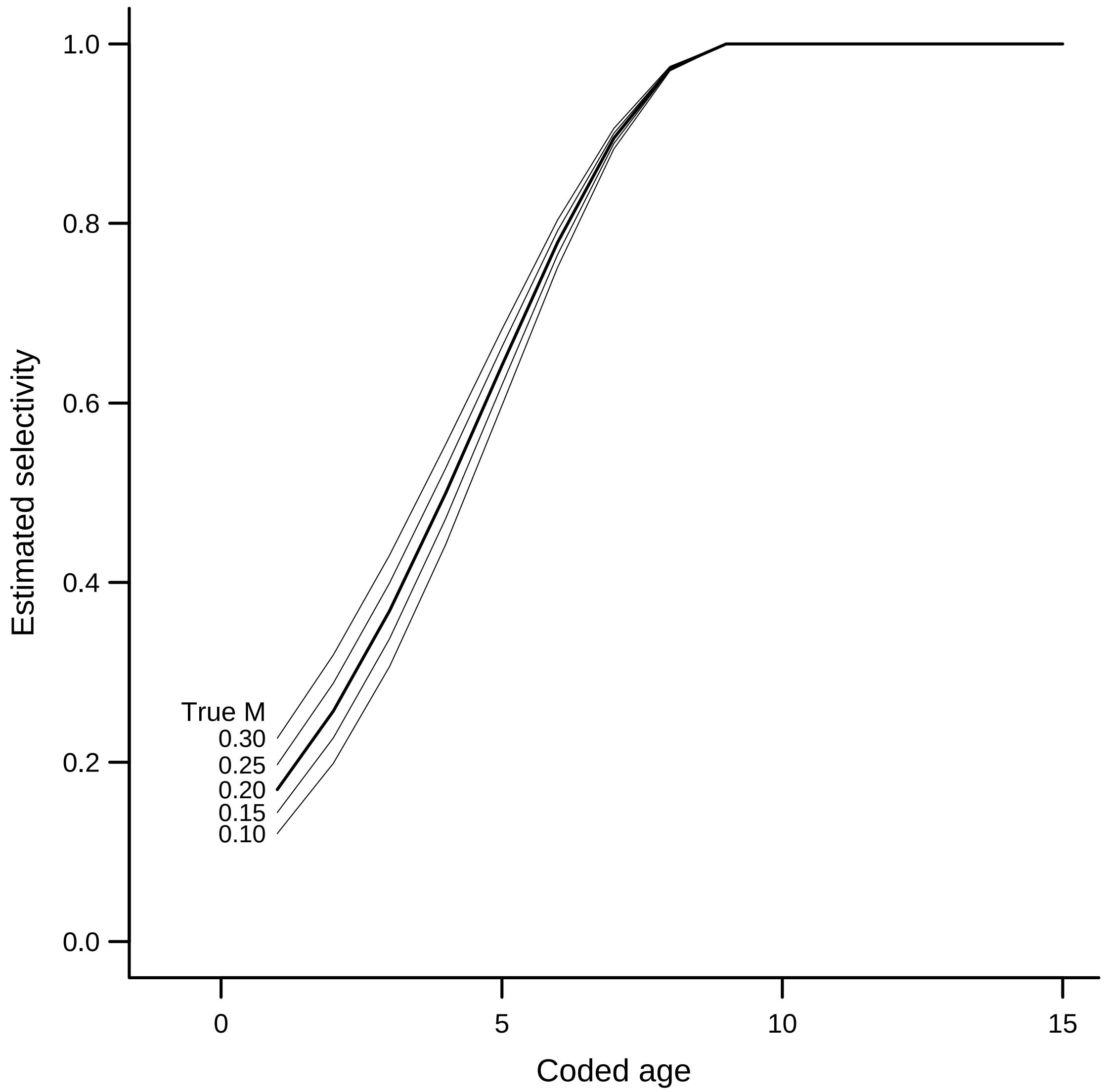

Figure 1. Fitted estimates of age-specific selectivity from Table 1. In every case fishing mortality was constant at F = 0.15 and the model was fitted with $\hat{M}$ = 0.20.

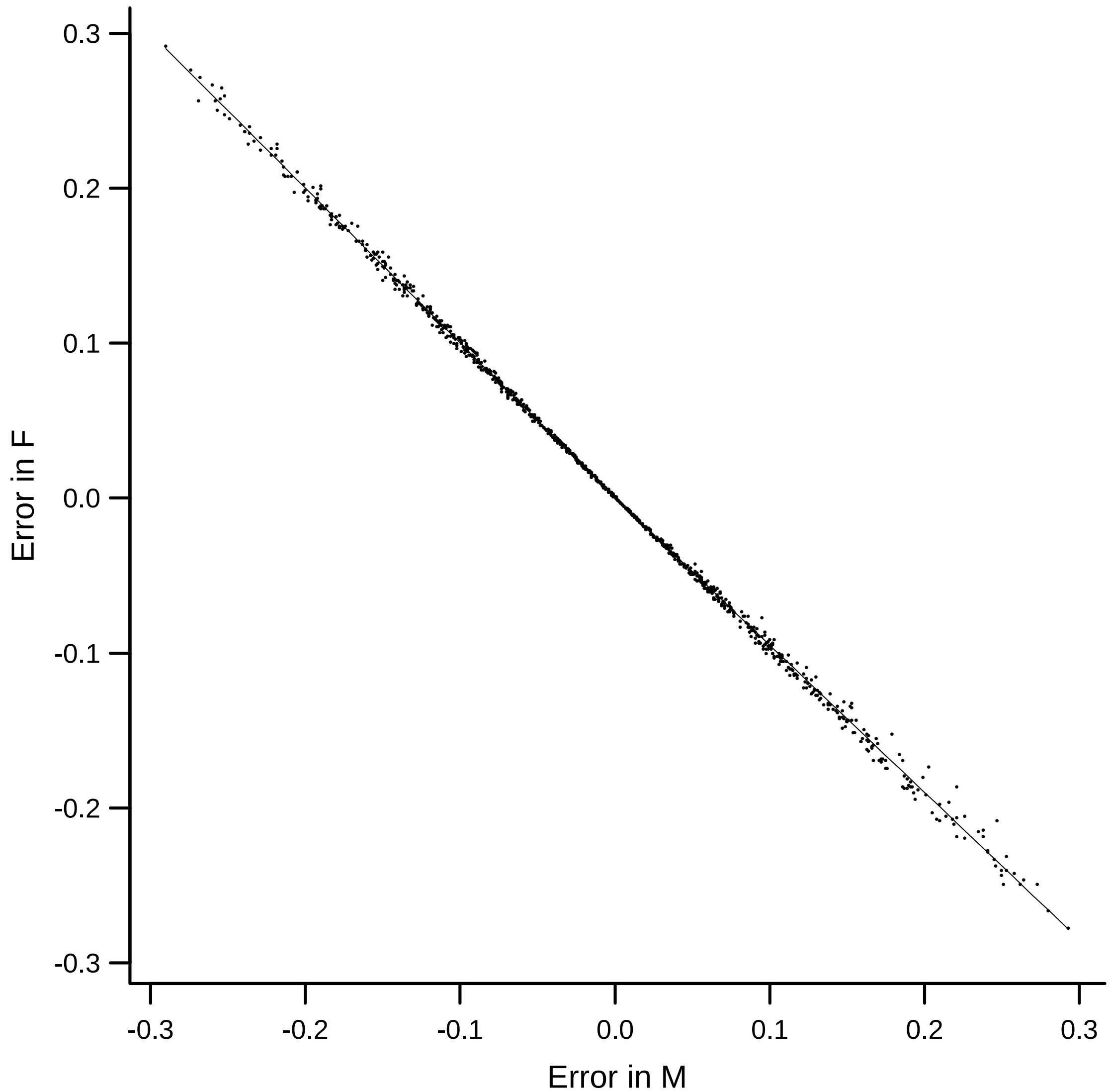

Figure 2. Effect of variable fishing mortality on fitted estimates of fishing mortality in 1000 simulations. For negative errors in M (that is, $\delta = \hat{M} - M < 0$), the regression line has slope –1.00. For positive δ the slope is –0.95.

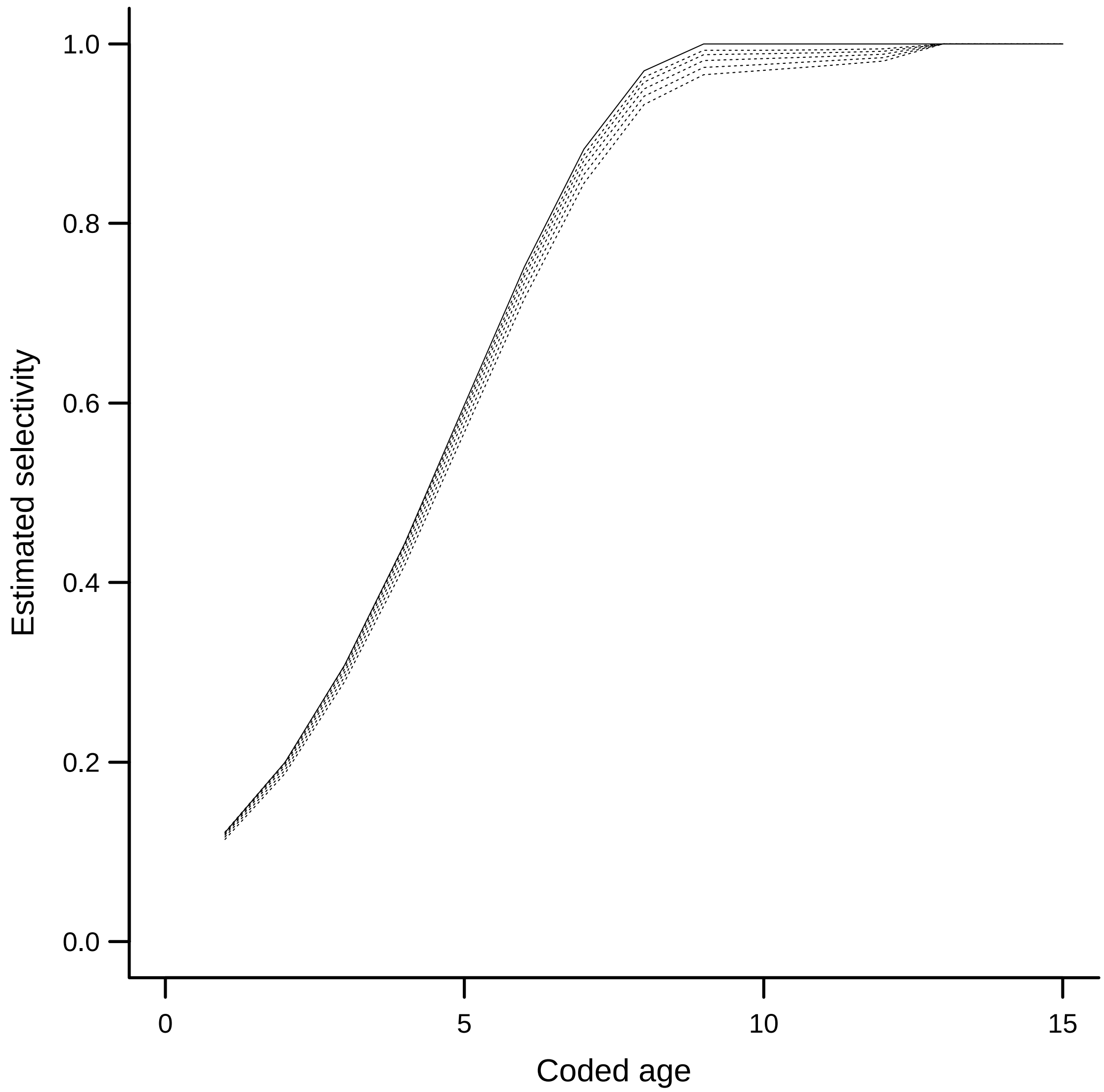

Figure 3. Effect of variability in fishing mortality on selectivity estimates when δ = 0.10 and $(F-\delta)$ is small. The uppermost (solid) line represents the case of constant F. The lines beneath it show the effect of variable F with $(F-\delta)$ = 0.20, 0.15, 0.10, 0.05, and 0 in descending order.

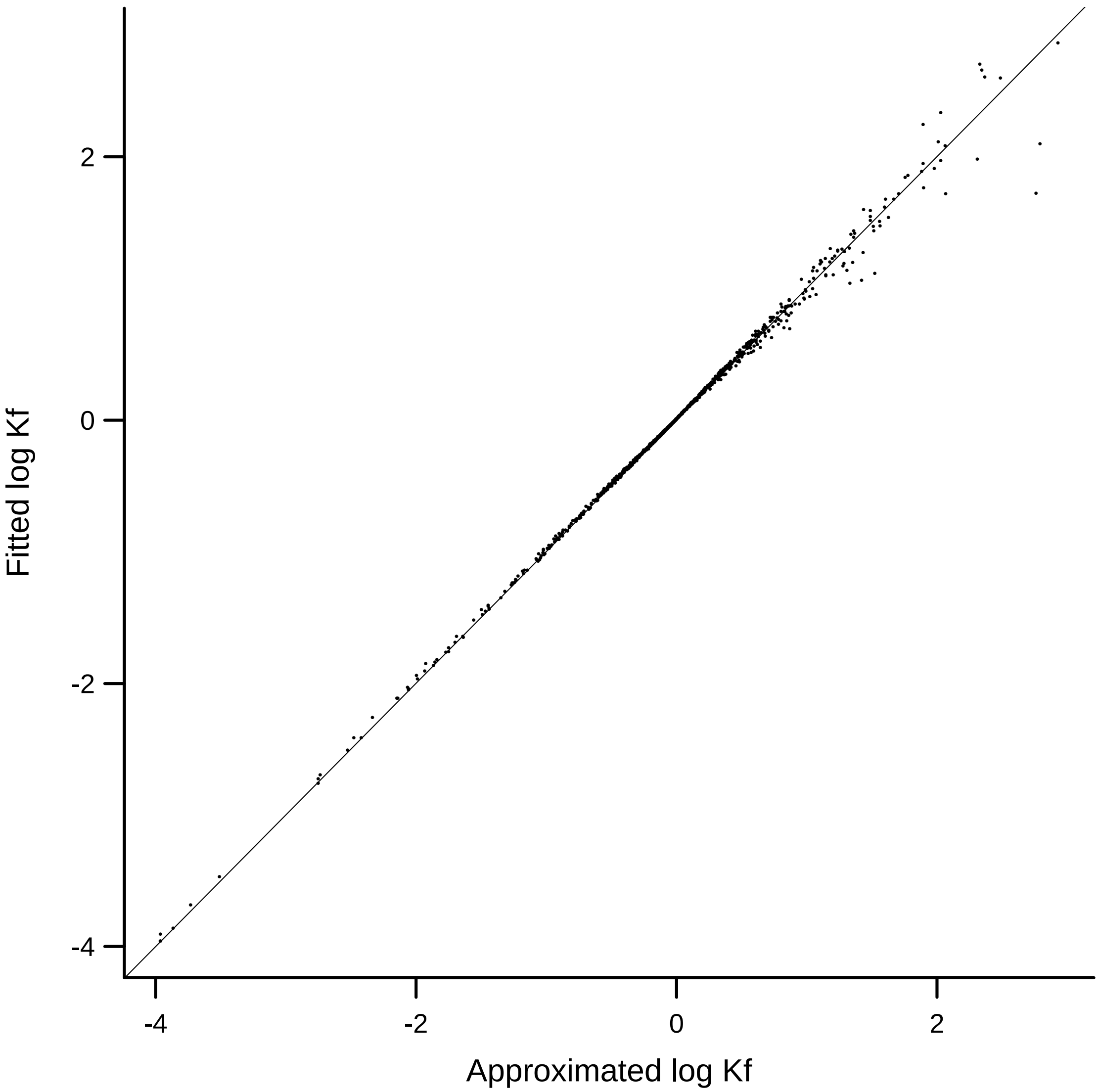

Figure 4a. Fitted and approximated values of $K_f = \hat{N}_f / N_f$ in 1000 simulations.

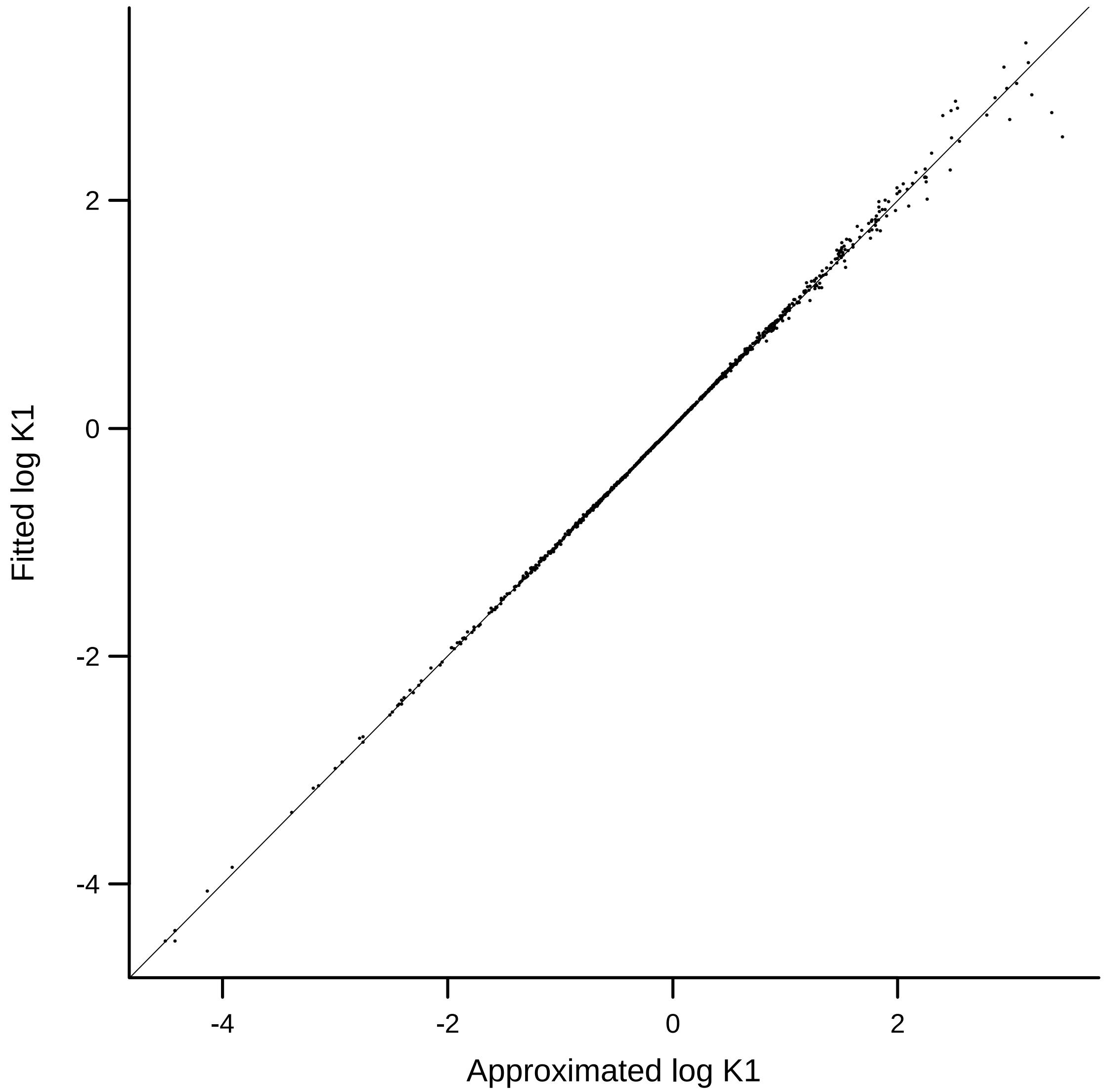

Figure 4b. Fitted and approximated values of $K_1 = \hat{N}_1 / N_1$ in 1000 simulations.

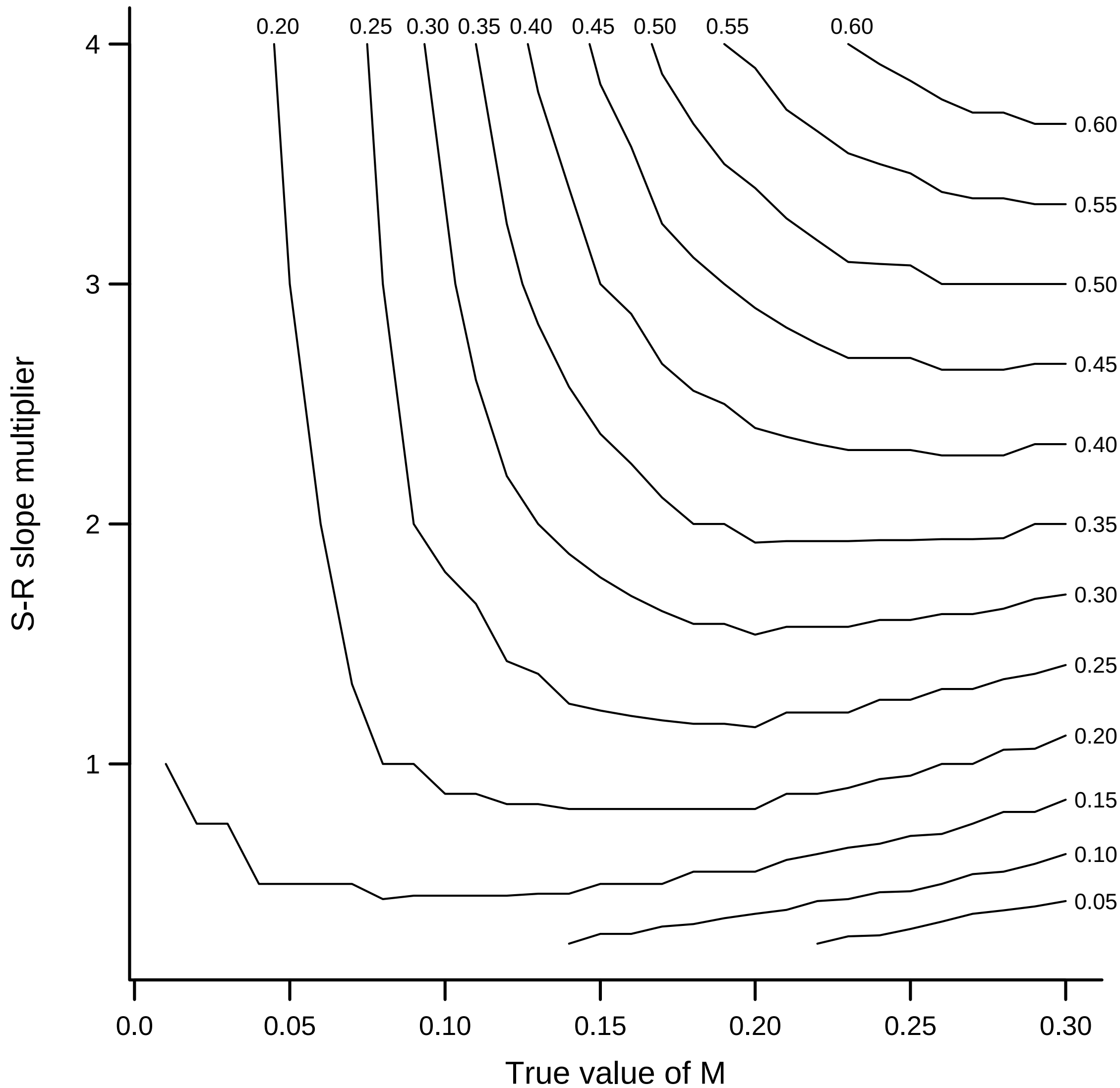

Figure 5. Contours of F_{MSY} as a function of true natural mortality rate *M* and a multiplier of the slope of the spawner-recruit (S-R) relationship used in this study.

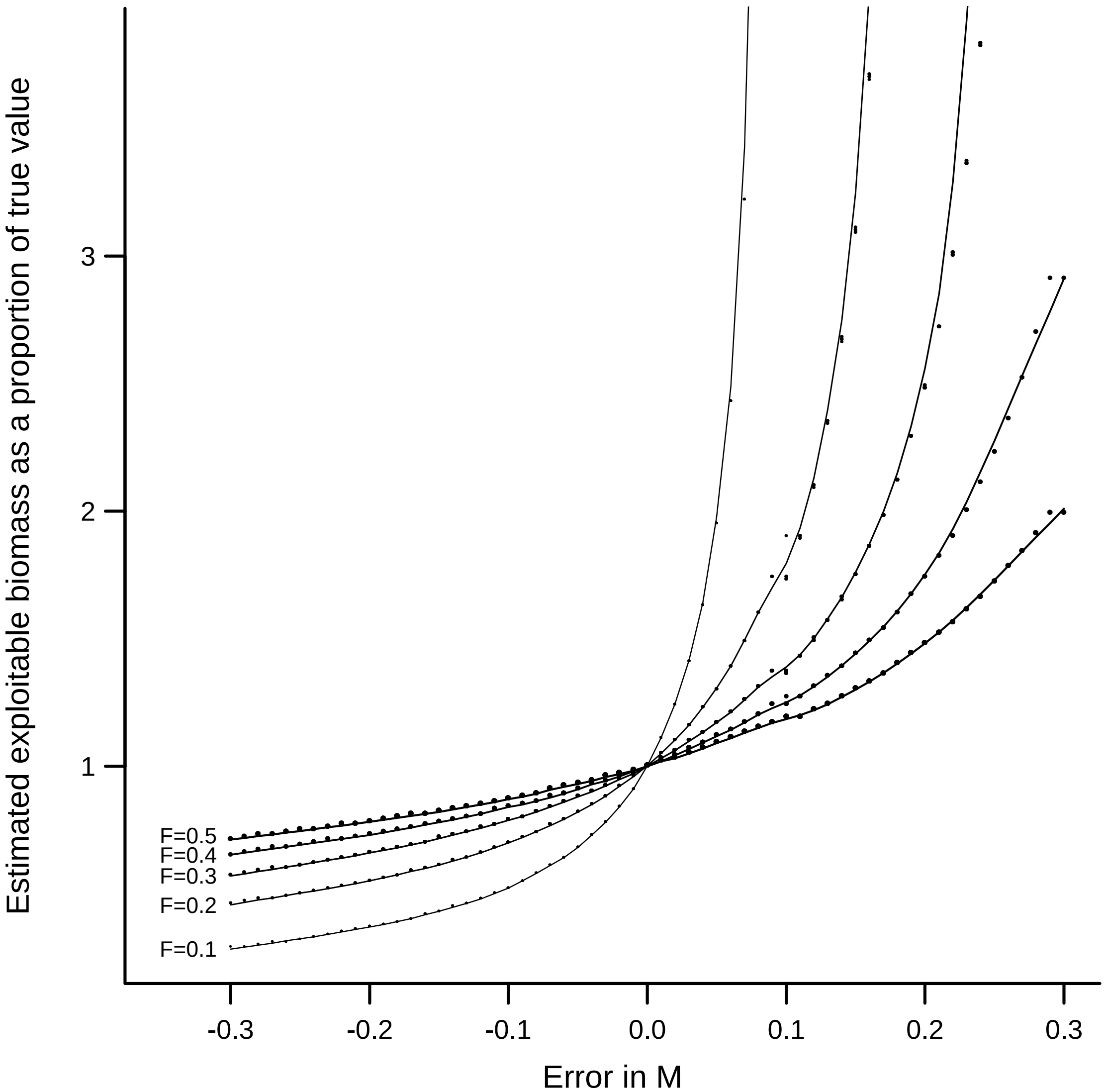

Figure 6. Estimated exploitable biomass as a proportion of the true value as a function of the error in estimated natural mortality, for average (historical) fishing mortality rates $\overline{F}$ =0.1, 0.2, 0.3, 0.4, 0.5. The thickness of the points and lines is an index of $\overline{F}$.

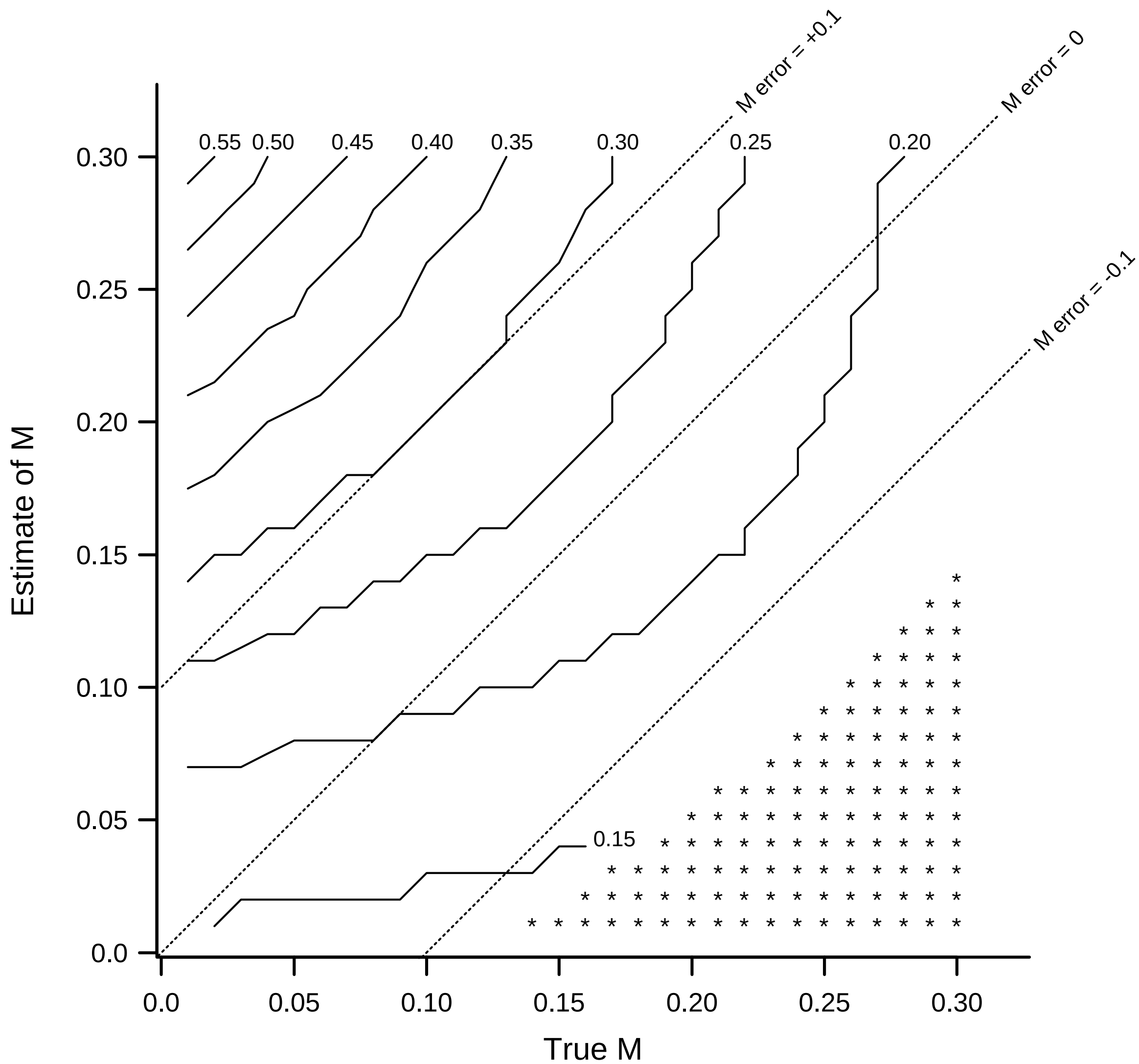

Figure 7a. Contours of the estimated value of F_{MSY} (at equilibrium) as a function of true and estimated natural mortality. The 1:1 line (labeled “M error = 0”) is the locus of the true value for a given natural morality rate. In the region marked with asterisks there is no equilibrium.

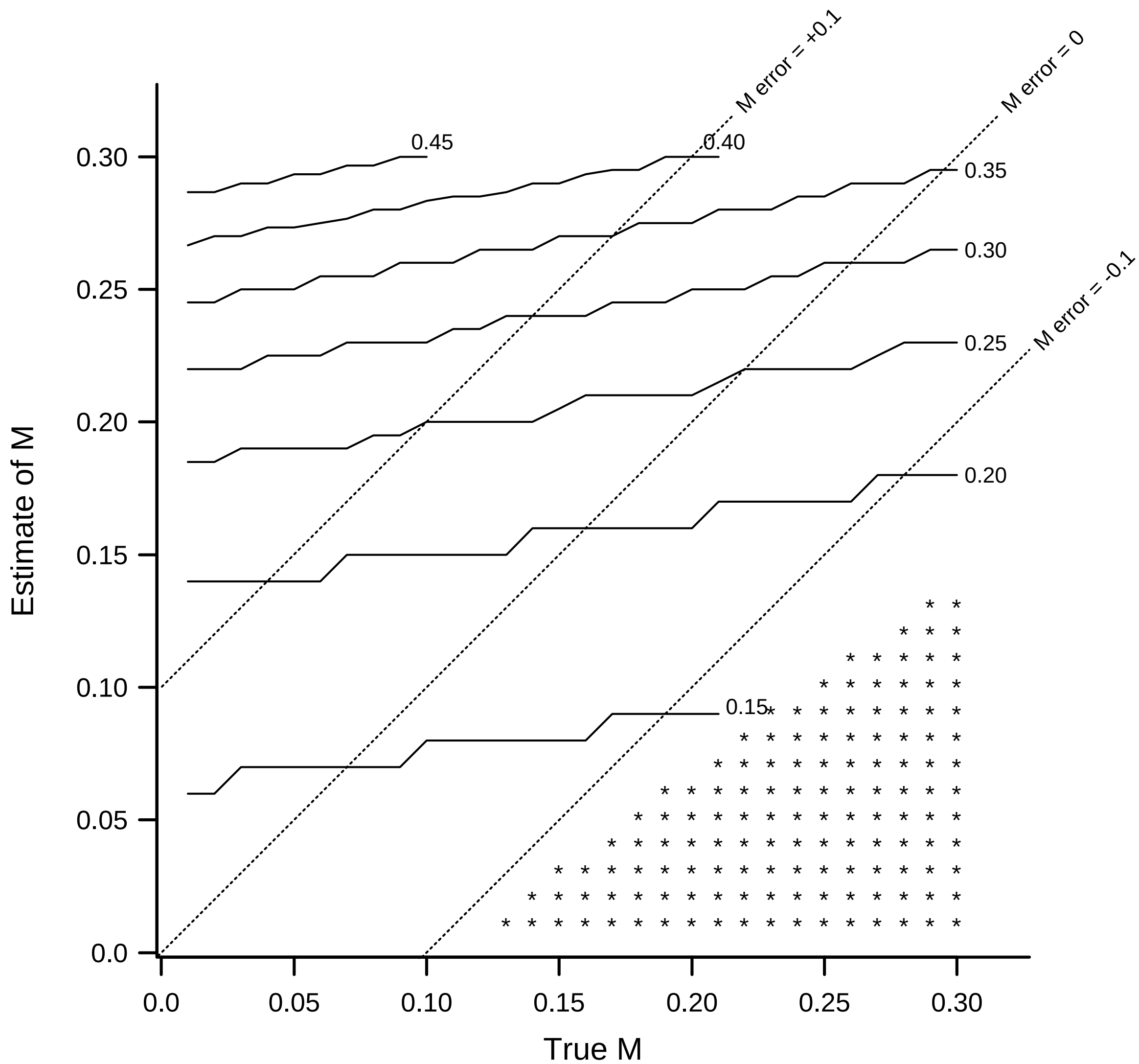

Figure 7b. Contours of the estimated value of $F_{35\%}$ (at equilibrium) as a function of true and estimated natural mortality.

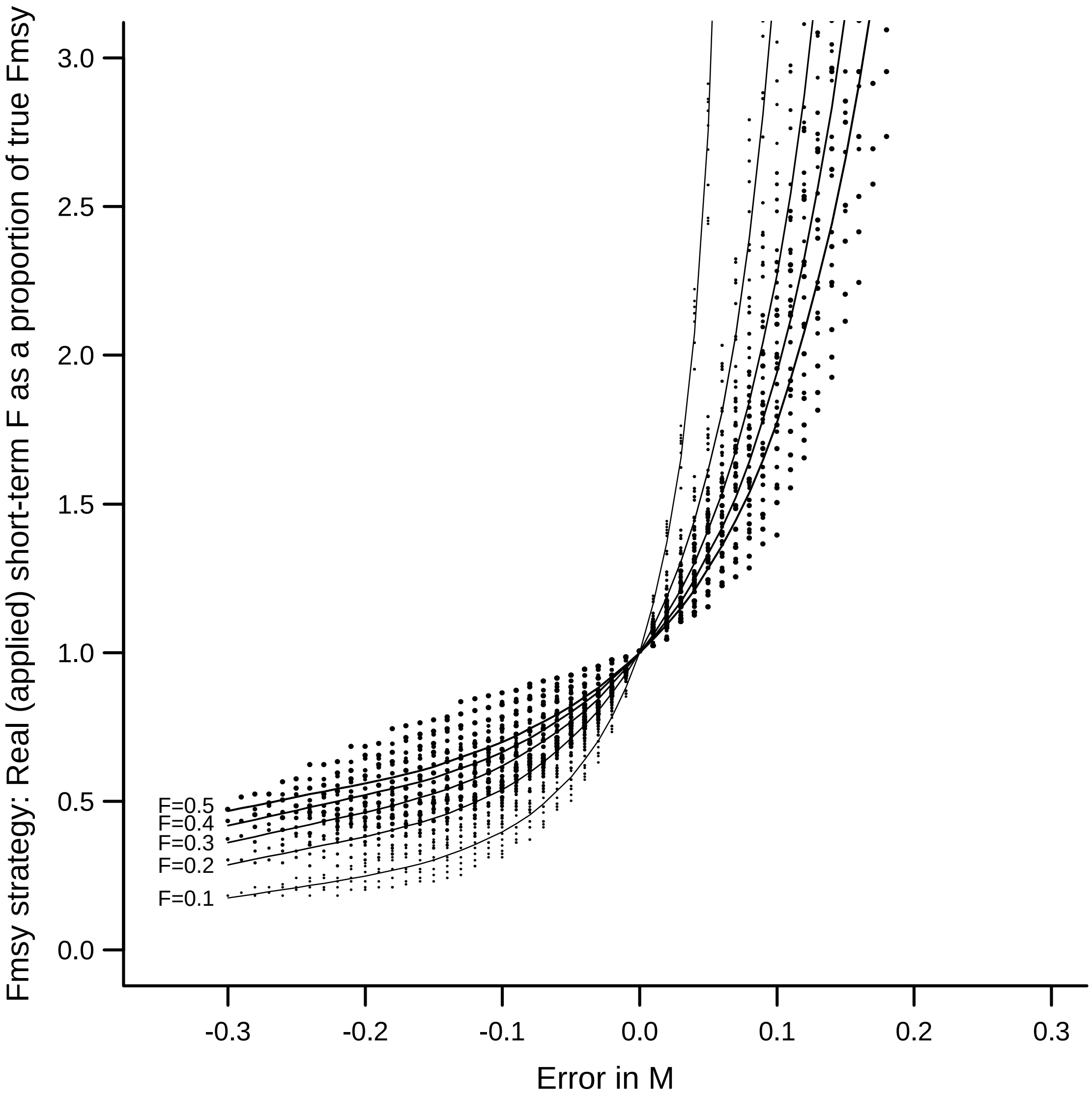

Figure 8a. Real short-term fishing mortality $\tilde{F}_1$ relative to F_{MSY} as a function of error in estimated natural mortality when the target harvest rate is F_{MSY}, for the cases plotted in Fig 6.

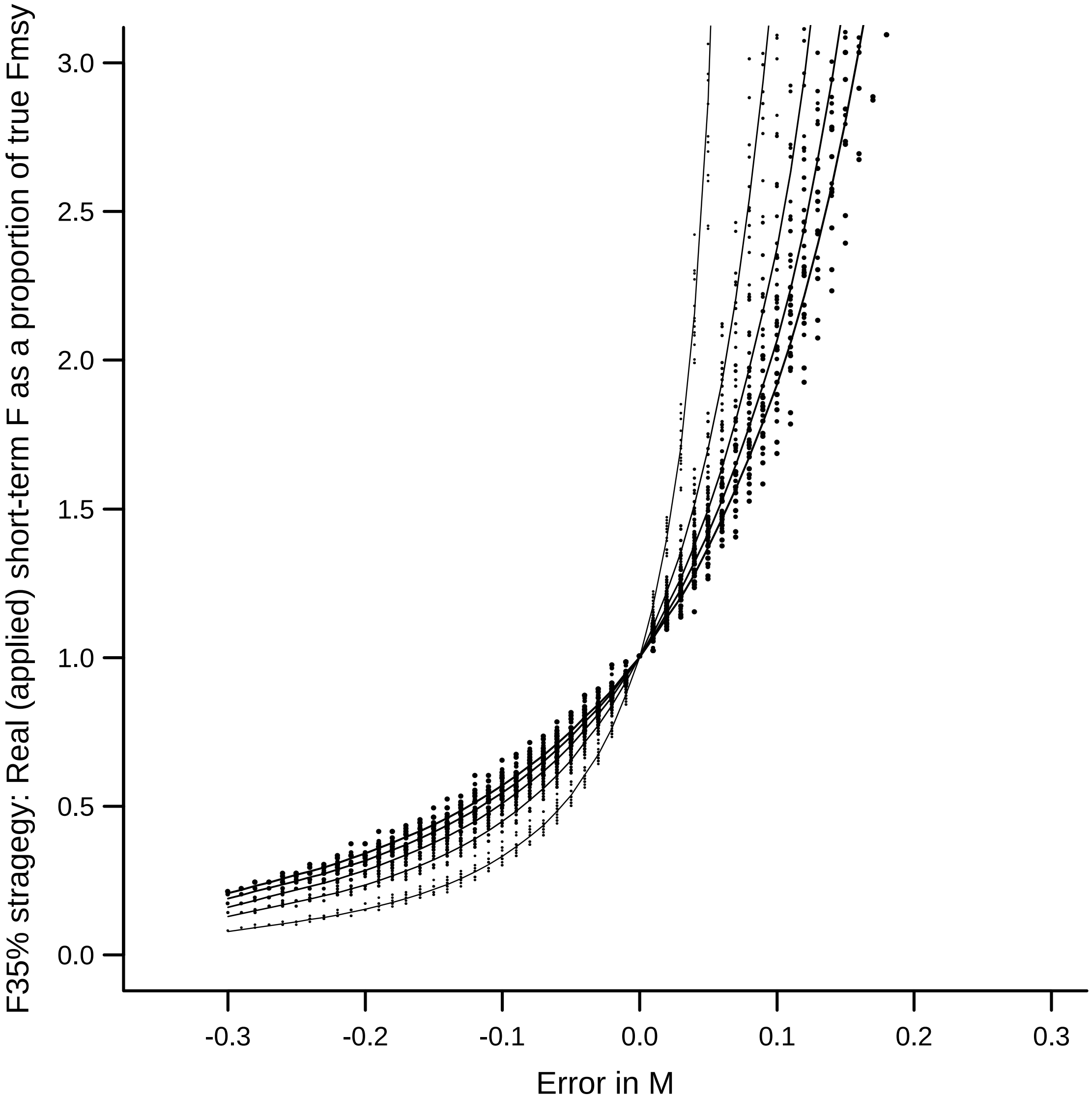

Figure 8b. Real short-term fishing morality $\tilde{F}_1$ relative to F_{MSY} as a function of error in estimated natural mortality when the target harvest rate is $F_{35\%}$, for the cases plotted in Fig 6.

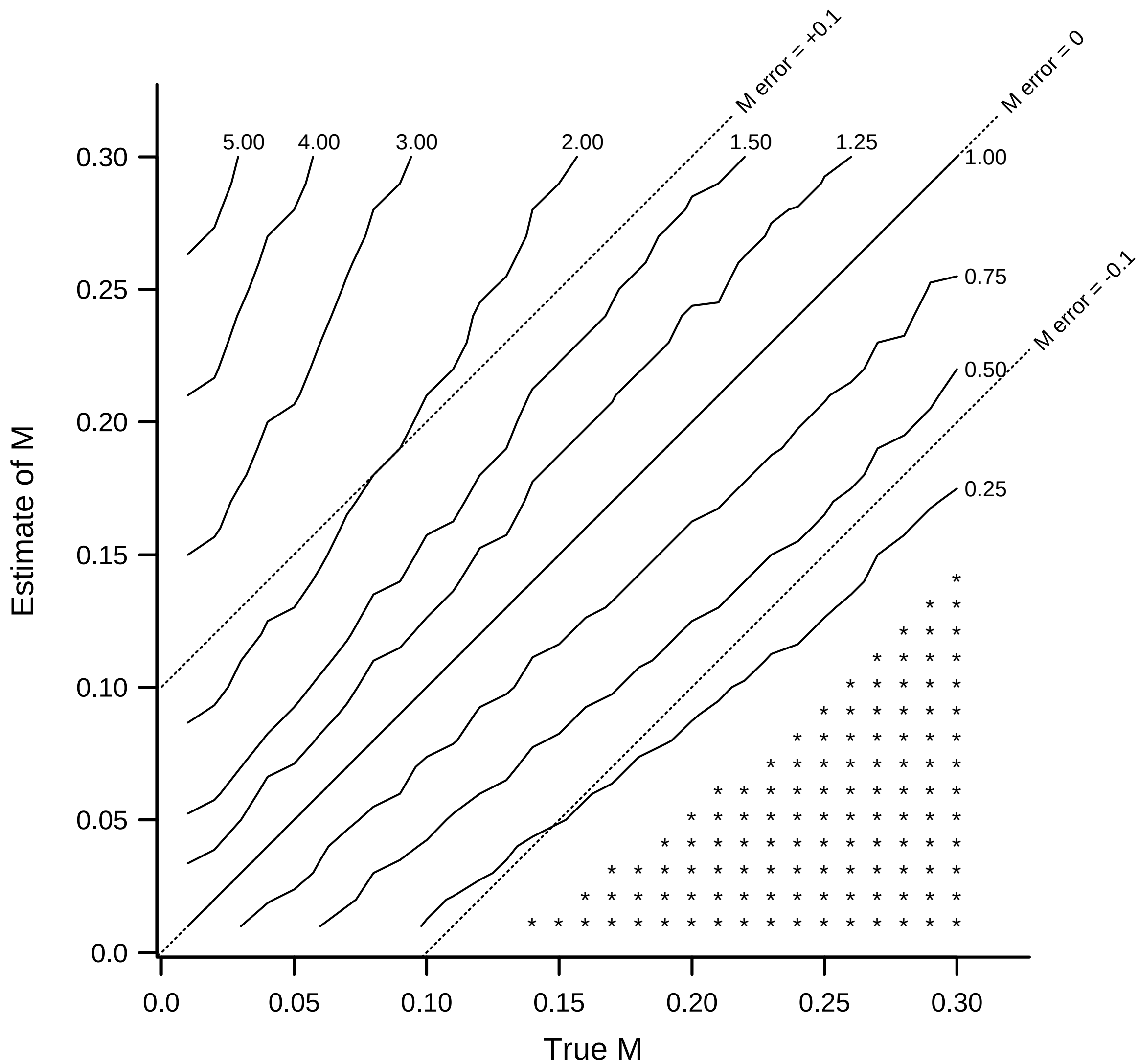

Figure 9a. Contours of real equilibrium fishing mortality $\tilde{F}_{eq}$ relative to F_{MSY} as a function of true and estimated natural mortality when the target harvest rate is F_{MSY} .

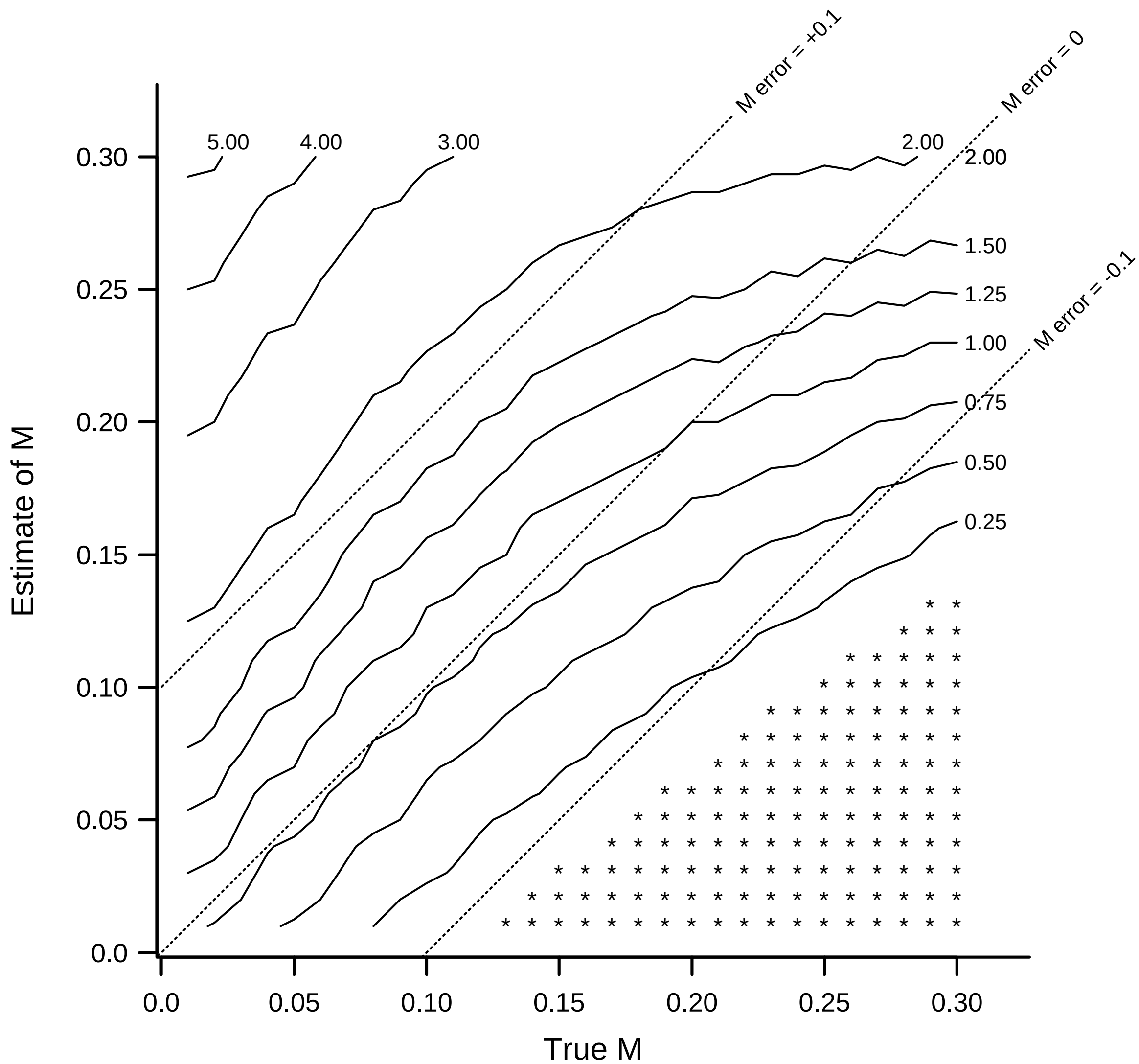

Figure 9b. Contours of real equilibrium fishing mortality $\tilde{F}_{eq}$ relative to F_{MSY} as a function of true and estimated natural mortality when the target harvest rate is $F_{35\%}$.

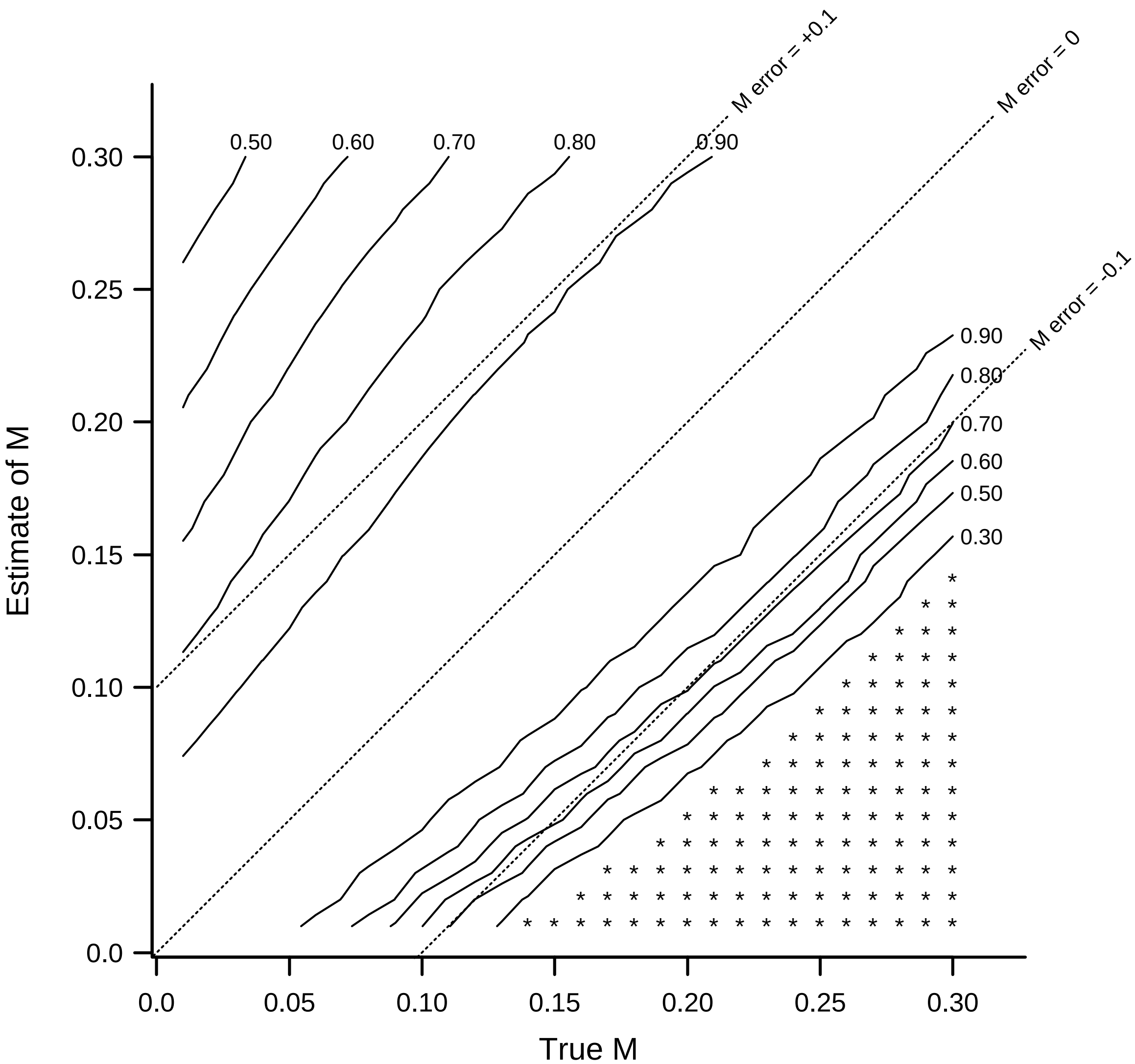

Figure 10a. Contours of equilibrium yield relative to MSY as a function of true and estimated natural mortality when the target harvest rate is F_{MSY} .

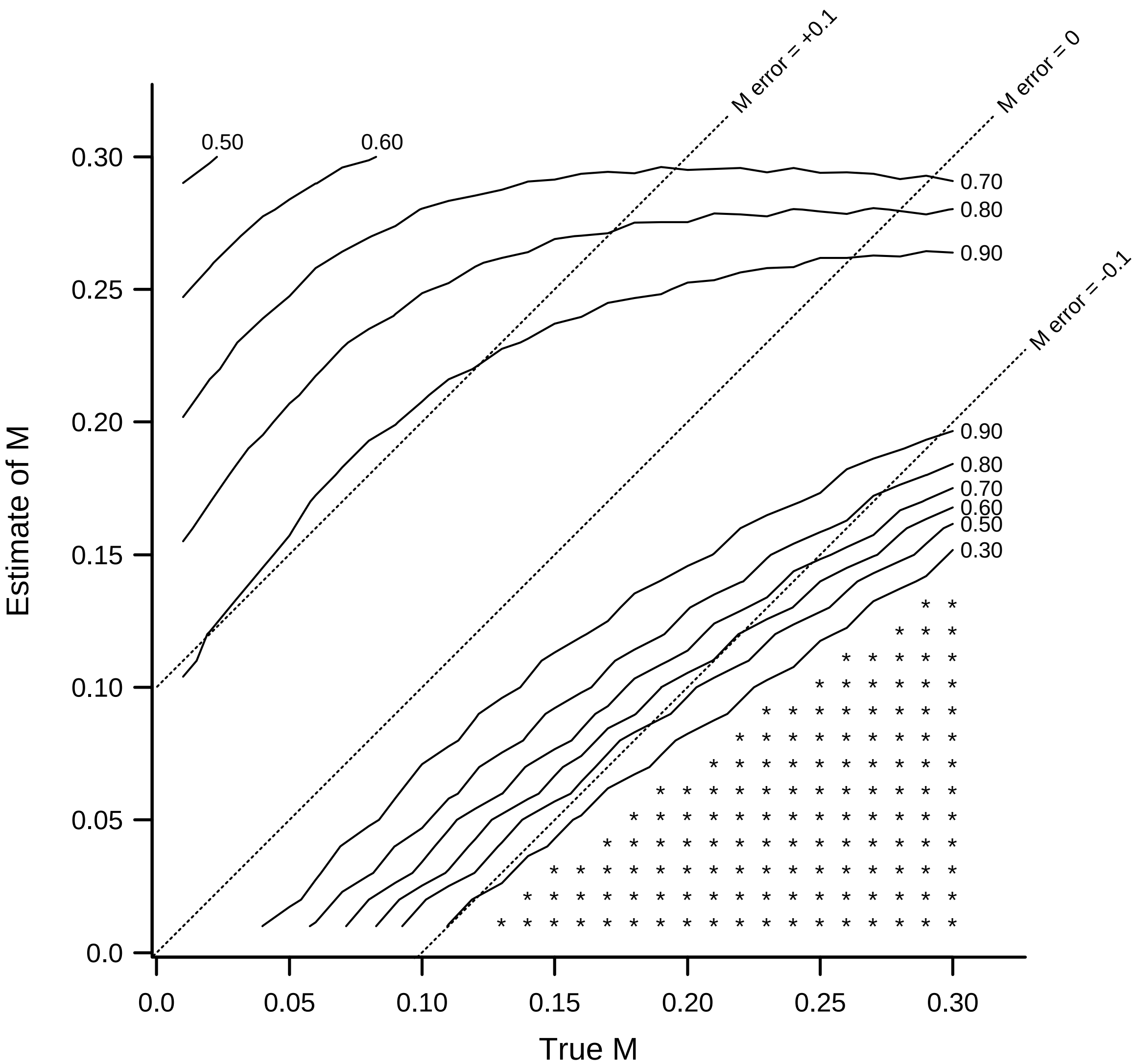

Figure 10b. Contours of equilibrium yield relative to MSY as a function of true and estimated natural mortality when the target harvest rate is $F_{35\%}$.

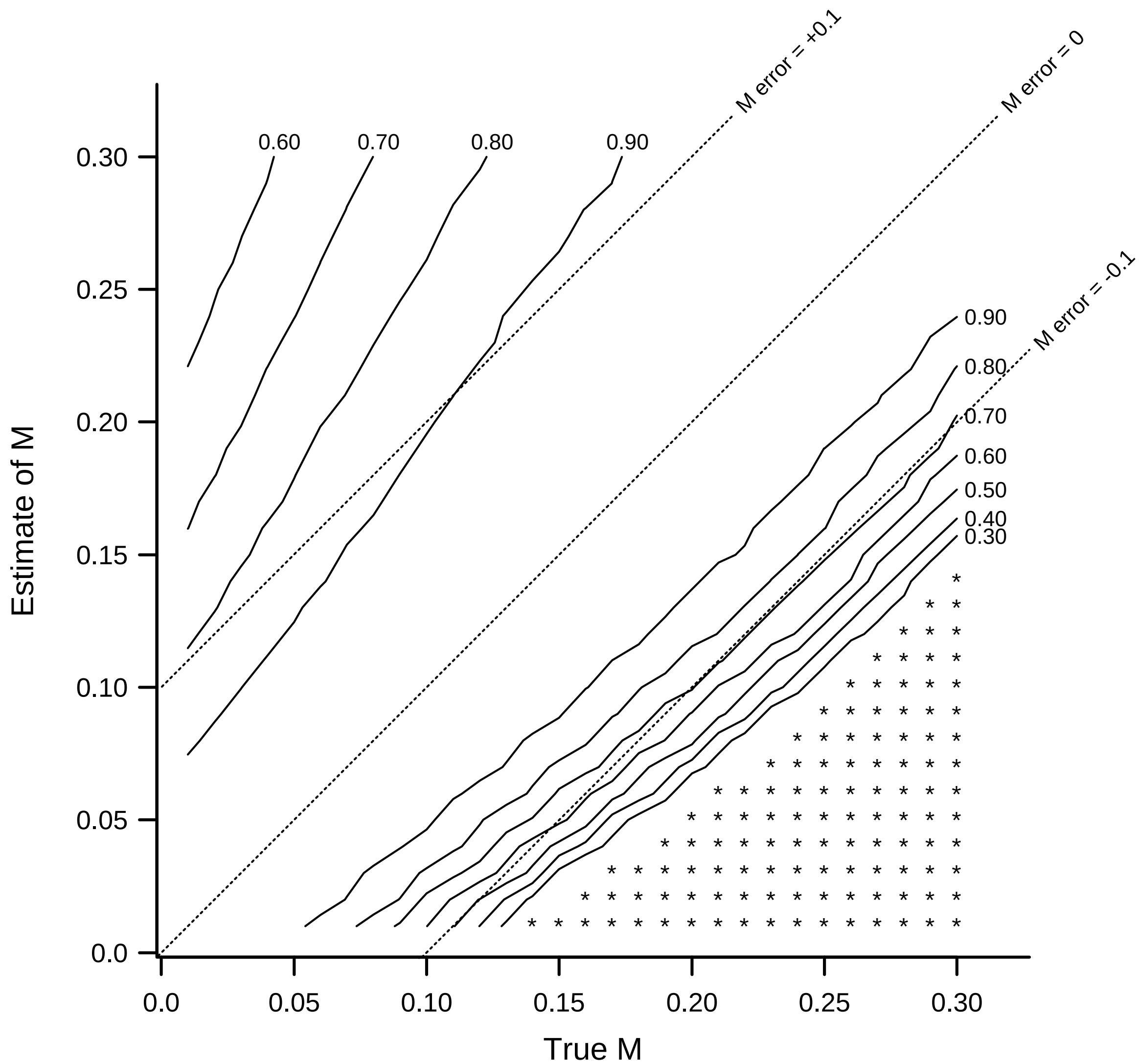

Figure 11. Contours of estimated MSY relative to true MSY as a function of true and estimated natural mortality.