YIELD-PER-RECRUIT MODELING OF A BRITISH COLUMBIA INTERTIDAL CLAM FISHERY: MANAGEMENT IMPLICATIONS OF SAMPLING DESIGN, VARIABLE RECRUITMENT, AND DATA COLLECTION BY USER GROUPS

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ABSTRACT

Invertebrate fisheries are becoming increasingly important in British Columbia (B.C.), but setting robust management strategies is difficult due to lack of data for stock assessment and poor understanding of invertebrate population dynamics. I applied Monte Carlo simulation to a butter clam (*Saxidomus giganteus*) fishery at Seal Island (near Courtenay, Vancouver Island, B.C.) to evaluate the effects of sampling methods, sample size, parameter estimation method, and variable recruitment on the accuracy and precision of input parameters to the Beverton-Holt yield-per-recruit (Y/R) model. The effects of this accuracy and precision on setting management strategies such as minimum legal size (MLS) with the Y/R model were evaluated by calculating the expected loss of Y/R and fishery value for each model scenario. Scenarios used one of four sampling methods, three methods of estimating total instantaneous mortality (Z) (Hoenig's method, Beverton-Holt method, and catch-curve analysis), and four levels of recruitment variability (including constant recruitment).

While uncertainty in the von Bertalanffy growth (VBGF) parameters alone resulted in small expected losses of Y/R (<10% maximum Y/R), uncertainty in instantaneous natural mortality, M, greatly increased expected losses (to between ~10% and ~60%). The effect of uncertainty in M was asymmetric; underestimating M gave greater expected losses than overestimating M. Furthermore, all three mortality estimation methods consistently underestimated Z, regardless of sampling method, sample size, or recruitment variability, indicating that losses in Y/R and fishery value will occur if estimates of Z are used to derive estimates of M.

Using a sampling method that increased detection of small clams increased the accuracy and precision of VBGF parameter estimates and therefore decreased expected losses of Y/R or fishery value. However, such a method would double sampling time and costs. Empirical estimates of the VBGF parameters from Seal Island (1980-1995) were precise enough to result in small losses of Y/R, indicating that they may not need to be estimated often (e.g., annually or bi-annually). However, these empirical estimates are likely biased because no method to detect small clams was used.

The Beverton-Holt method of estimating total mortality, Z, was the least biased of the three methods used. It was also relatively insensitive to sampling method, sample size, and violations of assumptions such as constant recruitment. However, empirical estimates of Z for Seal Island varied widely among survey years and estimation methods for several reasons. Unfortunately, lack of catch and effort data specific to Seal Island precludes estimation of M from empirical estimates of Z.

If $M > 0.1$, as empirical estimates of Z indicate, and harvest rates are low (~25%), the current MLS (63 mm) may be too high to maximize Y/R in the Seal Island butter clam fishery. However, the current MLS is probably insufficient to protect older, more fecund individuals (Neave 1944). Furthermore, differences in growth between populations (Quayle and Bourne 1972) may mean that management reference points should be set on a regional basis. Due to concerns related to recruitment overfishing as well as concerns of precautionary management, clam fishery managers should not lower the current MLS for butter clams. Finally, when decisions are to be made about shared responsibility for data collection between government agencies and user groups for intertidal clam stock assessment, several important implications should be considered (e.g., costs, precision, and accuracy of data) .

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Introduction

Although fin-fish management regulations are typically based on knowledge of detailed biology of fish species, such knowledge is often lacking for invertebrate species (Jamieson 1986, Urban 1998). Historically, British Columbia (B.C.) invertebrate fisheries were minor in both catch and value relative to major fin-fisheries such as salmon and groundfish. Therefore, they received little investment in data collection and monitoring, resulting in poor understanding of their biology and ecology (Bourne 1986, Jamieson 1986). However, the recent increasing value of several B.C. fisheries (e.g., geoduck, *Panope abrupta*; green sea urchin, *Strongylocentrotus droebachiensis*) has created new emphasis on invertebrate stock assessment (Harbo 1998). For example, unlike invertebrate stock assessment in previous years, explicit biological, management, and industry objectives are now required (Harbo 1998). Although this emphasis has resulted in significant changes in B.C. invertebrate fisheries management, there is still an inadequate understanding of the population dynamics of most species. Consequently, during the planning stage, the potential biological effects of management actions on invertebrate populations are often poorly understood.

The lack of formal evaluation of management strategies can result in sub-optimal regulations, in which invertebrate resources are either under- or over-harvested. While economic implications of both under-harvesting (e.g., failure to realize profits of larger harvests) and over-harvesting (e.g., loss of profitability when landings decline or a fishery closes) exist, over-harvesting may have serious biological consequences such as recruitment failure or extirpation. Therefore, a common biological management objective of invertebrate fisheries is to prevent or reduce the chance of growth and recruitment over-fishing.

To do this, most commercially important invertebrate species in British Columbia are passively managed with regulations that are enforceable at harvesting locations, which may be some distance from landing locations. Primary management tools are minimum legal sizes (MLSs), seasonal closures, area closures, and quotas in some fisheries (e.g., geoduck). Although passive regulations such as these are intended to prevent growth and recruitment overfishing by limiting fishing effort and protecting spawners (Watson et al. 1993), specific regulations are often not supported by quantitative analyses. For example, in many B.C. invertebrate fisheries the MLS is set so that individuals spawn at least once before being recruited to the fishery (Jamieson 1986), but for most B.C. invertebrate fisheries, the MLS is usually not rigorously evaluated against the biological or economic optimal level. To establish biological and management reference points which reduce risks of growth and recruitment overfishing (Caddy and Mahon 1995), fishery managers should quantitatively explore effects of various management strategies on population dynamics before they are implemented.

In non-invertebrate fisheries, yield-per-recruit (Y/R) models (Thompson and Bell 1934, Beverton and Holt 1957, Ricker 1975) are frequently used to evaluate management strategies. Therefore, they are appropriate to apply to invertebrate fisheries. Y/R models are based on the relationship among fishing mortality rate, survival rate (natural mortality rate), and somatic growth rate, and are typically used to evaluate different harvest rates for a given age- or size-at-entry, or vice versa. For example, Y/R analyses are commonly used with the objective of maximizing or optimizing biological yield to set management reference points such as F_{max} and $F_{0.1}$ (e.g., Zhang and Gunderson 1990, Govender 1995, Barbieri et al. 1997) or to evaluate current management regulations such as mesh size or MLS (e.g., Beverton and Holt 1957, Jensen 1981, Neilson and Bowering 1989, Kuikka et al. 1996).

Like all models though, the setting of management reference points based on the output of a Y/R model is sensitive to the values of input parameters. Furthermore, the accuracy and precision of these parameters depends on the methods used to estimate them as well as the quality of data. The Beverton-Holt Y/R model, a Y/R model which has been proposed for use in B.C. intertidal clam stock assessment (D. Heritage, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C. 1996, pers. comm), has seven input parameters. Parameters under direct control of fishery managers are the instantaneous rate of fishing mortality (F) and the age at which animals are first vulnerable to fishing (usually converted to size-at-entry, or MLS). Input parameters that are usually estimated empirically are the von Bertalanffy growth function (VBGF) parameters, the instantaneous natural mortality rate (M), and the total instantaneous mortality rate (Z). It is well established that Beverton-Holt Y/R curves are most sensitive to the value of M (Beverton and Holt 1957, Vetter 1988), a parameter which is notoriously difficult to accurately and precisely estimate (Vetter 1988, Pascual and Iribarne 1993). To a lesser extent, Y/R curves are also sensitive to values of the VBGF parameters (Beverton and Holt 1957). Although it is easier to accurately and precisely estimate VBGF parameters than M (Beverton and Holt 1957), somatic growth of invertebrates can be heavily influenced by environmental conditions (Butler 1953, Quayle and Bourne 1972, Weinberg and Helser 1996). Accurate and precise estimates of growth parameters are therefore important for Y/R analyses because differences in growth between populations will be reflected in Y/R model output (e.g., McShane and Naylor 1995). In addition, the magnitude of effect of the value of M on Y/R curves depends on the values of other Y/R parameters (Vetter 1988), further emphasizing the importance of accurate estimates of all Y/R input parameters.

Good parameter estimates depend on both the estimation method and the quality of data used. The effect of these factors on estimation of M and the VBGF parameters has been the focus of considerable attention in the literature. For example, many empirical models have been proposed for estimating M and Z (e.g., Beverton and Holt 1956, Ricker 1975, Pauly 1980, Hoenig 1983; see review in Vetter 1988). Subsequent research has examined the predictive power of some of these models (e.g., Pascual and Iribarne 1993, Vetter 1988), as well as the sensitivity of estimates to sampling errors, fitting methods, or to the violation of model assumptions (e.g., Paloheimo 1961, Ricker 1975, Majkowski 1982, Jensen 1984, Wetherall et al. 1987, Ralston 1989). Similarly, the estimation of VBGF parameters has received much attention. For example, research effort has focused on various methods of fitting different types of data to the VBGF (Vaughn and Kanciruk 1982; see review in Ricker 1975), alternative parameterizations of the VBGF that account for factors such as individual variability (Sainsbury 1980, Wang and Thomas 1995) or seasonal growth (Smith and McFarlane 1990), and statistical interpretation of VBGF parameters (Kimura 1980, Ratkowsky 1986, Cerrato 1990). Effort has also been directed at the effect of sampling biases such as aging error, sample size, and differential mortality on VBGF parameter estimates (Ricker 1969, Sainsbury 1980, Rowling and Reid 1992, Vaughn and Burton 1994, Castro and Lawing 1995).

Despite the considerable attention that has been devoted to developing methods for estimating M and the VBGF parameters, uncertainty in the values of these parameters is often ignored in Y/R analyses. Many authors estimate parameters or take point estimates from previous studies with little or no consideration of their accuracy or precision or the assumptions of the methods used. However, some authors present yield curves for more than one value of natural mortality or growth parameters, implicitly or explicitly acknowledging the underlying uncertainty in their values (e.g., Barbieri et al. 1997, Gribble and Dredge 1994, Ragonese and Bianchini 1996). Fewer authors discuss the management implications of this uncertainty. Similarly, mostly in modeling studies, other authors have purposely examined the sensitivity of Y/R models to errors in input parameters (Beverton and Holt 1957, Pelletier 1990, Pelletier and Gros 1991, Chen 1997) and have proposed methods for dealing with this uncertainty (Beverton 1965, Restrepo and Fox 1988, Clark 1994). However, with the exception of Pelletier and Gros (1991), none of these authors consider the effect of sampling design or estimation method on the potential bias and imprecision of the point estimates or frequency distributions they used. Pelletier and Gros (1991) explored the propagation of catch sampling errors in a Y/R model, using Virtual Population Analysis (VPA) to estimate F. However, both VPA and the complex sampling design they used require a quality and quantity of data not usually collected in invertebrate fisheries. Therefore, their results are not useful for data-limited invertebrate fisheries such as those in B.C. Tyler et al. (1989) examined the effects of aging errors on estimates of M and mean size-at-age and the propagation of this error in a Y/R model. Although they applied their approach to a sablefish (*Anoplopoma fimbria*) population and discussed the implications of such errors for overfishing, they did not discuss the implications for setting management regulations. No study that I know of has investigated the combination of the effect of sampling strategies on the accuracy and precision of parameter estimates, the propagation of this error in a Y/R model, and the implications of such errors for setting management strategies.

Therefore, the purpose of my research was to evaluate the management implications of various sampling designs that affect the accuracy and precision of estimates of parameters used in Beverton-Holt Y/R analysis. I used the operating model approach of Linhart and Zucchini (1986). This approach assesses the relative confidence that should be placed on a parameter estimate by evaluating how biased and uncertain (i.e. how precise) the estimate is (Hilborn and Walters 1992). The operating model describes the true (or assumed) dynamics of the system of interest and generates data from which parameter estimates are derived (Hilborn and Walters 1992). These parameter estimates are then compared with the "true" ones used in the operating model to determine bias and precision.

I applied this approach to the Seal Island butter clam (*Saxidomus giganteus*) fishery. Seal Island (near Courtenay, Vancouver Island, B.C.) supports a small commercial butter clam fishery (landings ≤40 metric tonnes/year) as well as First Nations and recreational fisheries. The butter clam fishery is currently managed with a 63 mm

MLS and seasonal and area closures. Decisions about harvest rates are not currently supported by quantitative assessments, but growing concern that heavy exploitation of legal sized clam resources may negatively affect recruitment and yield (R. Webb, Department of Fisheries and Oceans, Parksville, B.C., 1996, pers. comm) indicates that formal evaluation of management strategies is both necessary and appropriate.

Obviously, managers of invertebrate fisheries want the most accurate and precise parameter estimates possible for stock assessment, but budget constraints often limit the extent or quality of data collected. This is especially true of intertidal clam data collection, because harvested beaches are widely distributed and can be far from commercial processing centers. Therefore, intertidal clam fishery managers and biologists must make trade-offs between investment in data collection and quality and type of data collected, which will affect stock assessment results and therefore management decisions. Several sampling designs, with varying costs in time and money, have been used to collect intertidal clam data in British Columbia. In addition, different methods of estimating parameters require different types of data, some of which are more costly to obtain (e.g., age data). Therefore, I simulated four methods of data collection (sampling methods) and seven sample sizes in the operating model as well as three methods for estimating total instantaneous mortality (Z). Furthermore, because butter clam recruitment is extremely variable (Quayle and Bourne 1972, Paul and Feder 1973, Bourne 1986), I included log-normally distributed recruitment in the operating model and applied four levels of recruitment variability, including constant recruitment.

Reform in B.C. intertidal clam fishery management

Concerns over the adequacy of B.C. intertidal clam fishery management initiated changes in management beginning in 1989, when commercial clam licenses and area licencing were introduced. In 1991 the federal Department of Fisheries and Oceans (DFO) and the B.C. Ministry of Agriculture, Food, and Fisheries (MAFF) began working co-operatively on reforming the clam fishery. In 1992, DFO and MAFF jointly produced a discussion paper which described current clam fishery management and identified six key management concerns, including the lack of knowledge of harvesting impacts on clam survival and growth as well as concern with the existing MLSs (DFO and MAFF 1993). In their responses to this document, both the Sliammon First Nation and the Area C Clam Harvesters Association independently identified inadequate data and data-gathering methods on clam abundance as a problem for intertidal clam management (Dovetail Consulting Inc. 1997).

Traditionally, the Stock Assessment Division of DFO has been responsible for all intertidal clam stock assessment, including data collection and analysis. With the proposal and establishment of Community Management Boards[1] (CMBs) in some clam licence areas (e.g., Area F, the West Coast of Vancouver Island), however, stock assessment activities will be jointly undertaken by DFO and CMBs as soon as 1999 and will be solely completed by CMBs as soon as 2000 (Dovetail Consulting Inc. 1997). Current intertidal

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[1] Community Management Boards are multi-stakeholder groups (including commercial harvesters, First Nations, and federal and provincial management agencies) within a clam licence area with delegated authority for decision making over aspects of clam management (Dovetail Consulting Inc. 1997).

clam management plans between DFO and several B.C. First Nations (e.g., Council of the Haida Nation) require First Nations to assist in stock assessment activities (Harbo 1998), which include data collection, data analysis, and compiling results for management planning. For intertidal clams, data are typically collected for estimates of abundance and biomass as well as life history parameters such as growth and mortality parameters. Data analysis includes estimating such parameters from raw data and using these values in stock assessment models such as Y/R and stock-recruitment models. Finally, these results are presented to DFO managers and other clam fishery stakeholders and management plans are developed (see Dovetail Consulting Inc. 1997 for further detail).

Clearly, lack of data and data collection constraints are a key issue for all stakeholders in the management of intertidal clam fisheries. Understanding of the effect of accuracy and precision of parameter estimates on results of stock assessment modeling would be beneficial for improved stock assessment and conservation of invertebrate resources as well as for successful co-management of intertidal clam fisheries.

Methods

Historical surveys from Seal Island, B.C.

Approximately every three years since 1940, DFO biologists have used transect, random, or stratified random sampling designs to collect information on spatial distribution, abundance, and biomass of butter clams (D. Heritage, 1996, pers. comm) on Seal Island, B.C. I obtained morphological data for butter clams from Seal Island from D. Heritage (1996, pers. comm). These data included length, weight, and age data for surveys done in 1980, 1981, 1982, 1992, and 1995. Clams were sampled by digging substrate and hand-sorting the substrate. Lengths were recorded to the nearest mm, weights to the nearest gram, and age was determined by counting rings (winter growth checks) on the outer shell. Although butter clams do not spawn until late spring or summer (Fraser and Smith 1928, Quayle and Bourne 1972), all clams were assumed to have a birth date of January 01. Therefore, clams with one fully formed annulus were designated 1-year olds, those with two annuli as 2-year olds, etc.

Simulation Model

General description of the model

A generalized flow chart of the simulation model (Fig. 1) indicates its major components, which are described in detail below. First, the operating model simulated the dynamics of an age-structured butter clam population with 20 age-classes (butter clams > 20 years old rarely occur (Bourne 1987b)). The population dynamics model used either constant or stochastic, log-normally distributed recruitment. Simulations were 22 years long when recruitment was constant; this allowed the population to reach equilibrium. Simulations were 40 years long when recruitment was stochastic, but equilibrium was not achieved because the model did not involve dynamic feedback between the spawning population and recruitment. Second, the operating model sampled clams from the age structure of the final simulation year according to a specified sampling design (sampling method and sample size). Sampling was repeated 1000 times to generate 1000 data sets of aged clams. The sampling algorithm also assigned a length to each sampled clam (for each data set) based on its age and on a specified distribution around a mean length-at-age (according to the von Bertalanffy growth function with known parameter values). Third, the estimation model estimated growth and mortality parameters for each of the 1000 simulated data sets. Fourth, the model calculated Y/R at a given instantaneous fishing mortality rate, first with the true growth and natural mortality parameters, then with each of the 1000 sets of estimated growth parameters and an assumed value of the natural mortality rate. Fifth, the model estimated the optimal MLS (the MLS which maximized Y/R) for a given fishing mortality rate for both the true growth parameters as well as for each set of estimated VBGF parameters. Last, the model calculated expected loss (average weighted loss) in Y/R over the 1000 Monte Carlo trials.

Operating model

I used a standard age-structured population dynamics model (Hilborn and Walters 1992) with constant, age-independent natural mortality and constant fishing mortality. By assuming that the lowest of their estimates of Z for Seal Island butter clams approached natural mortality rates, Kingzett and Bourne (Department of Fisheries and Oceans, Nanaimo, B.C., 1995, unpublished results) estimated M for Seal Island butter clams to be 0.05-0.20. In addition, intertidal clam harvest rates have been set between 25% (F≈0.3) and 50% (F≈0.7) in recent years (R. Webb, 1996, pers. comm.). Therefore, unless otherwise stated, I used M=0.2 and F=0.3 in the operating model but also explored other parameter values in sensitivity analyses. Recruitment was either constant (300 000) or varied stochastically according to the log-normal recruitment term:

(1) $$R = \overline{R} \cdot e^{v}$$

where R is recruitment, $\bar{R}$ is mean recruitment (300 000), and v is a normally distributed random error term with standard deviation σ_v. In addition to constant recruitment ($\sigma_v = 0$), I modeled three levels of variability ($\sigma_v = 0.3$, 0.5, or 0.9). These levels were arbitrarily chosen, although two highest levels of σ_v modeled produced similar variability to what has been observed in intertidal clam populations (Quayle and Bourne 1972).

I assumed knife-edge recruitment to fishing based on a 63 mm MLS (current regulation) which was held constant for all simulation years. However, because I used an age-structured model, I modeled an age-specific vulnerability to fishing by considering variable size at age. Age-specific vulnerability was calculated as the proportion of clams in each age-class that are equal to or greater than the MLS, according to the von Bertalanffy growth function (VBGF) (von Bertalanffy 1938):

(2) $$L = L\infty \cdot \left(1 - e^{(-K \cdot (t - t_0))}\right) + w$$

where L is length (mm) at age t (yr), $L\infty$ is asymptotic length (mean maximum length) (mm), K is the Brody growth coefficient (rate of approach to $L\infty$) (unitless), t_0 is the hypothetical age at length 0 (yr) (assumed biologically unimportant), and w is a normally distributed error term with mean 0 and standard deviation σ_w.

To parameterize the VBGF in the operating model, I estimated the VBGF parameters from the 1995 Seal Island survey data ($N = 713$) using the non-linear fitting algorithm of SPSS 8.0 (1998) ($L\infty = 102.16$ mm, $K=0.1825$, $t_0=0.2156$ yr.). Standard deviation of the VBGF error term, $\sigma_w=5.0$ mm, was estimated as the mean of the standard deviations of the residuals from the best-fit VBGF for each of three Seal Island population surveys (1995, N=713; 1992, N=360, 1981, N=1029).

I assumed no handling-induced or incidental mortality (e.g. of non-harvested or non-sampled clams).

Sampling and data generation

Using a multinomial sampling algorithm (adapted from Press et al. 1989), N clams ($N = 50$, 100, 200, 500, 1000, 1500, or 2000) were sampled from the age distribution in the final simulation year of the population dynamics model according to one of four sampling methods. The operating model then randomly assigned a length to each clam based on its age, using the VBGF (Eqn. 2) with parameters described above. The model did not take into account spatial sampling design.

Intertidal clams are sampled by digging and hand-sorting substrate, but very small clams are often missed using this method. This results in under-representation of clams of the youngest age-classes, which can affect abundance, recruitment, and growth parameter estimates. Experiments at Savary Island, B.C. have shown that manila clams (*Tapes philippinarum*) <20 mm long are often not detected by hand-sorting (G. Gillespie et al. Department of Fisheries and Oceans, Nanaimo, B.C., 1995, unpublished results) but are detected when substrate is sieved through a 3 mm mesh. Therefore, in the base case sampling method (referred to as D20 below), the operating model applied a "lower detection limit"; clams <20 mm were not sampled (these clams were "returned" to the population and a new sample drawn). However, to overcome under-representation of the youngest age-classes, DFO biologists have recently employed two methods for improving detection of smaller clams; (1) sieving substrate through a mesh or (2) turning the top 10 cm of substrate (where smaller clams occur) onto a white tarp and hand-sorting this substrate (R. Lauzier, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C. 1998, pers. comm). Therefore, the second sampling method was identical to the base case design (D20) but without a lower detection limit. With this representative sampling method (referred to as RS below), the probability of sampling a clam of a certain age was equal to the probability of occurrence of that age in the population.

On beaches where intense harvesting has occurred, few large clams are found. Because lack of data from the oldest age-classes can bias VBGF estimates (Sainsbury 1980), in other simulations both the D20 and RS methods were modified so that extra clams in the oldest age-classes were sampled in addition to the *n* previously sampled clams (referred to as D20-X and RS-X). Extra clams were sampled to give a total of five clams in age-classes 15-20 yr. (inclusive). These two sampling methods (D20-X and RS-X) were used only for the estimation of VBGF parameters.

Estimation model

The model estimated the VBGF parameters and total instantaneous mortality (Z) for each data set of sampled clams. VBGF parameters were estimated from all data points using a non-linear, Levenberg-Marquardt least-squares routine (adapted from Press et al. 1989). Z was estimated using three methods, each previously used in a DFO intertidal clam stock assessment, and each with fairly modest data requirements but requiring different types of data.

First, Z was estimated using Hoenig's method based on maximum age (Hoenig 1983):

$$\ln\left(\hat{Z}\right) = a + b \cdot \left(\ln\left(T_{\max}\right)\right) \tag{3}$$

where T_{max} is the age (yr) of the oldest individual in the sample, and a and b (1.23 and -0.832, respectively) are fitting parameters Hoenig estimated from natural mortality and maximum age data for 28 mollusc populations of 13 species.

Second, Z was estimated using the length-based Beverton-Holt method (Beverton and Holt 1956):

$$\hat{Z} = K \cdot \frac{\left(L\infty - l_{bar}\right)}{\left(l_{bar} - l_{crit}\right)} \tag{4}$$

where l_{bar} is the mean length of clams above l_{crit} , the length-at-entry to the fishery, or MLS (mm).

Third, Z was estimated using catch-curve analysis (Ricker 1975), where Z is estimated from linear regression as the negative slope of the descending limb of log(frequency) vs. age. Because catch or sample age frequency distributions rarely show an even (i.e., straight) descending limb, the estimation model applied a rule to determine the first age-class used in the catch-curve regression: one year plus the median age of recruitment to the fishery (determined using the VBGF parameter estimates and the true MLS). Ricker (1975) suggests this as appropriate when recruitment to the fishery is "fairly abrupt" (i.e., between two and five years).

Percentage bias was calculated, for both VBGF and mortality parameter estimates, as:

(5) $$\frac{\left(\hat{P}-P\right)}{P}\cdot 100\,\%$$

where $\hat{P}$ is the parameter estimate and P is the true value used in the operating model.

Yield-per-recruit

For each of the 1000 sets of estimated VBGF parameters, yield-per-recruit (Y/R) was calculated according to the Beverton-Holt equation (Beverton and Holt 1957):

(6)

where Y/R is yield-per-recruit (g), F is instantaneous fishing mortality, M is instantaneous natural mortality (assumed not to change from its historical value), Z is total instantaneous mortality (Z = F + M), and $r = t - t_0$ (yr). True values of parameters (used in the operating model) were used in Eqn. 6 to calculate the true Y/R curve (Y/R over a range of MLSs for a given F), and for each Monte Carlo trial, estimates of parameters were used to calculate an estimated Y/R curve (over the same range of MLSs for the same F as the true Y/R curve).

W∞ was calculated from estimates of L∞ using the allometric growth relationship:

(7) $$W\infty = a\cdot\left(L\infty\right)^{b}$$

where a and b are parameters that were estimated from length and weight data from the 1995 Seal Island survey using the non-linear fitting algorithm of SPSS 8.0 (1998) (0.000207 and 3.089, respectively). Although the Y/R model assumes isometric growth (i.e., b=3 (Eqn. 7), Beverton and Holt 1957, Ricker 1975), because I am interested in relative, not absolute, differences in Y/R, departure from the assumption of isometric growth should not affect interpretation of model results. Furthermore, the error in relative differences in Y/R is much smaller than in absolute differences when $b \neq 3$ (Ricker 1975).

Expected loss

With perfect knowledge of the parameter values of the Y/R model, the optimal MLS (the MLS that maximizes Y/R for a given fishing mortality rate, F) can be determined. Using the true VBGF parameter values from the operating model, I calculated the optimal MLS for a particular fishing mortality rate, F = 0.3, at the true natural mortality rate, M. This was the true optimal MLS (true MLS_{opt}). Obviously, in practice, the true values of Y/R input parameters are unknown and uncertainty about their values will usually result in an estimate of MLS_{opt} (estimated MLS_{opt}) that deviates from the true MLS_{opt}. However, the probability of occurrence of a particular magnitude of deviation between the true and estimated MLS_{opt} depends on the values of parameters estimated from the clam population, which in turn depend on the particular statistical sampling and estimation methods used. A sub-optimal MLS will result in some loss of Y/R because it is not the MLS which maximizes Y/R; this loss is referred to as opportunity loss (Raiffa 1968). A loss function can then be characterized by determining the loss associated with each of several possible deviations of estimated optimal MLSs around the true MLS_{opt} (see Frederick and Peterman 1995 for further discussion of expected loss).

For each model run, or "scenario" (level of variable recruitment, sampling method, and sample size), the model estimated the MLS_{opt} for each of the 1000 Monte Carlo trials using the estimated VBGF parameter values for each trial (but assuming, in this particular set of simulations, perfect knowledge of values of M, F, and Z, an assumption that will be relaxed in a later set of simulations). This gave a frequency distribution of estimated optimal MLSs. The model then calculated the percent loss in Y/R associated with each estimated MLS_{opt} as the difference between Y/R at the true MLS_{opt} (maximum Y/R) and Y/R at the estimated MLS_{opt}, divided by the maximum true Y/R. The average of the 1000 estimates of loss gave the expected percent loss of Y/R associated with that particular model scenario (this is the same as multiplying the loss associated with each deviation from the true MLS_{opt} by its probability of occurrence and summing these weighted losses). I refer to this expected loss as the <u>expected percent loss of Y/R due to uncertainty in the VBGF parameters</u>.

In addition to calculating expected loss where only the VBGF parameters are uncertain, I also calculated expected loss where both the VBGF parameters and M are uncertain. I did this by repeating the above 1000 Monte Carlo simulations for calculating the MLS_{opt} for each of nine possible values of M. Expected loss calculated in this manner is then particular to the assumed value of M; I calculated expected loss for a range of assumed values of M around the true value of M to generate a curve of expected losses (due to uncertainty in the VBGF parameter estimates and inaccurate estimates of M) for each model scenario. These expected loss curves show the additional loss associated with inaccurate estimates of M. I refer to this expected loss as the <u>expected percent loss of Y/R due to uncertainty in the VBGF parameters and inaccurate estimates of M</u>.

Results

von Bertalanffy parameter estimates

Simulation results indicated that with representative sampling (RS), L_∞ was well estimated regardless of the true recruitment situation. K was also well estimated except at the highest level of simulated variability in recruitment ($\sigma_v = 0.9$, Eqn. 1) where it was underestimated by up to 18% (at the largest sample size, N=2000). However, at all levels of recruitment variability, the base case sampling method (D20) resulted in noticeable bias in L_∞ (Fig. 2); at the highest level of variability ($\sigma_v = 0.9$, Eqn. 1), L_∞ was overestimated by ~7% and K was underestimated by ~21% at sample sizes ≥ 100 (at $N = 50$ estimates were even more biased). Of the four sampling methods, representative sampling (RS) method gave the most accurate estimates of L_∞ and K (Fig. 2). Collecting extras clams in the oldest age-classes (RS-X) increased the precision of estimates but did not affect their accuracy. Increasing sample size also increased precision but did not affect accuracy of all sampling methods with the exception of the D20-X method. This method was more accurate than the base case method (D20) at small sample sizes, but with increasing sample size, L_∞ was increasingly overestimated and K increasingly underestimated.

Increasing either the true level of M or F in the operating model slightly decreased the precision of estimates of L_∞ and K. Under constant recruitment, increasing either M or F resulted in decreasing accuracy of VBGF parameter estimates, but under variable recruitment no trend in increasing or decreasing accuracy was discernible (statistics not shown).

Total instantaneous mortality estimates

Precision of Z estimates was unaffected by the level of recruitment variability for all three estimation methods (Fig. 3). However, increasing recruitment variability affected the accuracy of the three mortality estimation methods differently (Fig. 3). Increasing recruitment variability decreased the accuracy of both Hoenig's method and to a lesser extent, the catch-curve method. Conversely, increasing recruitment variability increased accuracy of the Beverton-Holt method. Because true recruitment of the butter clam is highly variable (Quayle and Bourne 1972), only the highest level of recruitment variability ($\sigma_v = 0.9$ in Eqn. 1) was used in simulations for expected loss calculations.

Increasing sample size increased precision of all three methods for estimating Z (Fig. 4), with Hoenig's method being most precise. Catch-curve analysis was least precise when sample sizes < 500 but the Beverton-Holt method was more precise than catch-curve analysis at $N \geq 500$. Increasing sample size did not affect accuracy of the Beverton-Holt method much, but it did increase accuracy of the catch-curve method and decrease accuracy of Hoenig's method (Fig. 4).

Unlike the VBGF parameter estimates, accuracy and precision of all three mortality estimates were not affected by removing the lower detection limit (i.e., there was no major difference between D20 and RS sampling methods) (Fig. 4).

Except at very low levels of true natural mortality, M, and fishing mortality, F, all three estimation methods consistently underestimated Z (Fig. 5). Increasing the level of M for a given F and vice versa decreased both the precision and accuracy of all three methods. Although it was the most precise, Hoenig's method grossly underestimated Z even in scenarios where the catch-curve and Beverton-Holt methods performed reasonably well (Fig. 3, 4, 5).

Expected losses due to uncertainty in VBGF parameters

For a particular model scenario, the estimated MLS_{opt} was variable across Monte Carlo trials, but the 1000 estimates were normally distributed (e.g., Fig. 6). The amount of variability (i.e., the range of estimated optimal MLSs) depended on the sampling method and sample size (results not shown) whereas the mean deviation of the estimated optimal MLS from the true MLS_{opt} depended on the assumed value of M. The mean estimated MLS_{opt} was not significantly different from the true MLS_{opt} when the correct value of M was used (Fig. 6, t-test, P=0.99, N=1000).

All four sampling methods resulted in at least some loss in Y/R due to sampling for the estimation of VBGF parameters (Fig. 7, again, here M is assumed known). However, losses greater than 10% occurred only at sample sizes ≤ 200 with the base case sampling method (D20).

Expected losses of the sampling methods depended on sample size (Fig. 7). With the exception of the D20-X method, expected loss due to uncertainty in the VBGF parameters decreased with increasing sample size. However, at sample sizes ≥ 500, expected losses were negligible (<2% of the maximum Y/R) when either of the representative sampling methods (RS or RS-X) was used. Between these two methods, collecting extra clams in the oldest age-classes reduced expected loss only at small sample sizes (≤ 500); for example, at sample size = 100, expected loss was reduced from 3.9% to 0.5% by collecting extra clams.

I also calculated an approximate expected loss of Seal Island fishery value, but this was based on indirect estimates of value because catch statistics specific to Seal Island have not been kept since 1963. However, annual butter clam landings in DFO Statistical Area 14, of which Seal Island butter clams are believed to account for 50-75% (D. Heritage, 1996, pers. comm.), range between ~5 and ~50 metric tonnes between 1980 and 1994. In spring 1998, forty metric tonnes of butter clams were harvested from Seal Island (R. Webb, 1998, pers. comm). This harvest is therefore probably one of the largest to occur on Seal Island in recent years. The landed value of this spring 1998 harvest was approximately Can$230,000 (at $0.53/kg., R. Webb, 1998, pers. comm). If the parameter values used in the operating model reflect true conditions, then the optimal MLS suggested by this combination of parameters, 62 mm, is almost identical to the current MLS, 63 mm. Under these conditions, it is reasonable to assume that the spring 1998 fishery maximized Y/R. Therefore, assuming that 40 tonnes represents the maximum fishery yield, then multiplying percent expected loss of Y/R by $230,000 gives the expected loss of Seal Island fishery value.

Expected loss due to uncertainty in VBGF <u>and</u> inaccurate estimates of M

Using an inaccurate estimate of M to estimate MLS_{opt} along with uncertainty in VBGF parameters had a marked effect on expected losses. All four sampling methods resulted in asymmetric expected loss curves, with underestimates of M resulting in higher expected losses than overestimates of M (Fig. 8). For a sample size of 500, the degree of asymmetry in expected loss curves differed depending on the sampling method used to obtain the VBGF parameter estimates. Both methods with representative sampling (RS and RS-X) behaved similarly, showing the minimum expected loss at the true level of M (i.e., when loss occurs only due to uncertainty in VBGF parameter estimates) and less asymmetry than sampling with a lower detection limit (D20 or D20-X). Both methods that incorporated a lower detection limit showed highly asymmetric loss curves with minima at assumed values of M greater than the true value of M.

Increasing sample size generally decreased expected loss at most assumed values of M for both the base case method (D20) and representative sampling (RS) (Fig. 9), however, the largest decreases in expected loss occurred at the smallest sample sizes (e.g., 50 to 200).

The value of M affected the shape of the expected loss curve (Fig. 10). Increasing M for a given F increased the asymmetry of the expected loss curve by increasing expected loss for a given underestimate of the true M and decreasing expected loss for a given overestimate of M. Increasing F had no effect on the shape of the expected loss curve (Fig. 10).

Empirical parameter estimates from Seal Island survey data

Empirical parameter estimates from Seal Island survey data showed wide variability. Sample size between survey years varied greatly (Table 1), as did VBGF parameter estimates. Estimates of Z also varied between years, but the Beverton-Holt and catch-curve methods of estimating total mortality, Z, gave similar results for any survey year except 1990 when the catch-curve estimate was extremely low ($Z = 0.057$). Hoenig's method gave the highest estimate of Z in each survey year.

Assuming M and F are constant (0.2 and 0.3, respectively), the optimal MLS (MLS_{opt}) suggested by each set of VBGF parameter estimates from Seal Island varied between 58 and 62 mm (Table 1). However, for a given set of VBGF parameter values (e.g., those from the 1995 Seal Island survey, which were used in the operating model), MLS_{opt} depends on the values of M and F, with lower values of MLS_{opt} occurring at higher levels of natural mortality but higher values of MLS_{opt} occurring at higher levels of fishing mortality (Fig. 11).

Discussion

Simulation results indicate that while uncertainty in VBGF parameters will result in loss of Y/R and fishery value (Fig. 7), inaccurate estimates of M have a much greater effect on the magnitude of these losses (Fig. 8). However, M is notoriously difficult to estimate accurately (Vetter 1988, Pascual and Iribarne 1993) and as well, results here show that underestimating M results in greater losses of yield-per-recruit and fishery values than overestimating M by an equal amount (Figs. 8, 9, 10). The implications of this are great, because simulation results also showed that all three methods of estimating mortality consistently underestimated Z (Fig. 3, 4). Underestimates of Z occurred regardless of sampling method, sample size, and historical rates of natural mortality (M) or fishing mortality (F).

Interpreting simulation results

Estimating the VBGF parameters

The optimal MLS is the MLS that maximizes Y/R at a particular rate of fishing mortality, F. For a given value of M, the shape and scale of the Y/R curve is affected by the value of the VBGF parameters. If VBGF parameter estimates are biased enough, the estimated MLS_{opt} will deviate from the true MLS_{opt}. In such cases, uncertainty in VBGF parameters will result in loss of Y/R because Y/R is not maximized at the estimated MLS_{opt}. Simulation results indicate that sampling method affects the accuracy of VBGF parameter estimates (e.g., the base case sampling method (D20) gave biased estimates of $L\infty$ and K, see Fig. 2). Although Knight (1968), Sainsbury (1980), Rowling and Reid (1992), and others acknowledge that variability in length at age and unrepresentative sampling can bias VBGF parameter estimates, only Castro and Lawing (1995) have attempted an extensive evaluation of the effects of sampling schemes and sample sizes on VBGF parameter estimates. Using Monte Carlo simulation modeling, they concluded that proportional allocation (i.e., sampling length classes in proportion to their occurrence in the true population - what I call representative sampling) tended to give more precise estimates than simple random sampling (of individuals of all lengths) or fixed allocation sampling (where fixed numbers of individuals were sampled in pre-defined length strata). They also showed that although fixed allocation sampling ensured that small and large individuals were sampled, it did not improve VBGF parameter estimation; instead, it gave the most biased estimates of the three sampling designs. Unlike my results though, increasing sample size in their study did not result in any clear trends. However, Castro and Lawing (1995) used a very small number of Monte Carlo trials (100), small sample sizes (46-200), and disregarded any estimates of $L\infty$ or K that fell outside a range of "acceptable" values for the species they studied. Therefore, their results are somewhat inconclusive.

Unlike Castro and Lawing (1995), my results show that both sampling design and sample size strongly affected the accuracy and precision of VBGF parameter estimates. These effects are clearly reflected in estimates of expected loss for the four sampling designs at different sample sizes (Fig. 6). Under-representative sampling of the youngest age-classes (i.e., sampling with a lower detection limit) biased $L\infty$ up and K down, probably because there are insufficient data for the steepest part of the growth curve and K (the rate of approach to $L\infty$) is therefore poorly estimated. It is not surprising that K is consistently underestimated when $L\infty$ is overestimated, because most non-linear fitting techniques result in strong negative co-variation between estimates of $L\infty$ and K (Xiao 1994) (not to be confused with co-variation between K and $L\infty$ in different populations of the same species, which also exists (Xiao 1994)). However, this bias resulted in overestimates of MLS_{opt}, meaning that individuals are not harvested at a small enough size to maximize Y/R. Therefore, loss in yield and fishery value resulted, and the expected loss (average loss over 1000 Monte Carlo trials) was greater at any given sample size than it was for representative sampling (which gave unbiased estimates of $L\infty$ and K). Even lower expected losses occurred when representative sampling was augmented by collecting extra clams (RS-X), because of the increased precision of VBGF parameter estimates. Similarly, for these three sampling designs, increasing sample size decreased expected loss because of the increased precision of VBGF parameter estimates. However, increasing sample size increased expected loss when extra clams were collected in conjunction with the lower detection limit. This occurred because of the interaction of the lower detection limit, which gave biased estimates of the VBGF parameters, and the sampling algorithim for collecting extra clams in the operating model, which only sampled extra clams in the oldest age-classes if less than five clams had previously been sampled (ensuring that $n = 5$ in the six oldest age-classes). At small sample sizes (e.g., $N = 50$) few, if any, clams were sampled in the oldest age-classes. Therefore, the model sampled up to 30 extra clams (five individuals for each of six age classes), which increased accuracy and precision of the VBGF parameter estimates because (1) total sample size was effectively increased and (2) data near the asymptote of the VBGF were collected. With increasing sample size, however, the benefits of collecting extra data diminished because fewer extra clams needed to be sampled to fulfill the requirement of $n = 5$. Therefore, total sample size did not increase as much as at smaller sample sizes and less data near the asymptote of the VBGF were collected (because they had already been collected). Consequently, the bias in estimates of $L\infty$ and K created by the lower detection limit increased and expected loss therefore increased. However, the simulated version of this sampling routine is flawed because ages of clams are not known immediately when sampled on the beach. It is more likely that researchers would collect extra clams in the largest length classes instead of the oldest age classes, and length is not as well correlated with age in the oldest age classes as it is in younger age classes.

The consistent asymmetry in the expected loss (due to uncertainty in VBGF parameters and inaccurate estimates of M) curves is attributable to the effect of M on the magnitude of MLS_{opt}. With increasing natural mortality, the true MLS_{opt} decreased because it pays to harvest animals before they die of natural causes. Therefore, all other parameter values being equal, overestimating M will cause MLS_{opt} to be underestimated, and vice versa. The Y/R loss curve (Fig. 5) is itself asymmetric (due to the non-linearity of the Beverton-Holt Y/R model), with an overestimate of MLS_{opt} giving a greater loss of Y/R than an underestimate of MLS_{opt} of the same amount. Therefore, for a particular sampling method and sample size, underestimating M shifted the distribution of estimated optimal MLSs (created by sampling for VBGF parameters) towards larger values and the resulting expected loss was greater because the steeper side of the loss curve (Fig. 6) was more heavily weighted than the flatter side.

Estimating total instantaneous mortality, Z

Obtaining the most accurate estimates of mortality rates possible is extremely important because simulation results showed that underestimates of M result in greater expected losses of fishery yield and value than overestimates of M. The Beverton-Holt method of estimating mortality gave the most accurate estimates of Z of the three methods considered in this study. Furthermore, it was the most robust estimator, being least sensitive to sample size and to violations of key assumptions. The Beverton-Holt method is also attractive for use in stock assessment because, unlike Hoenig's method and catch-curve analysis, it does not require aging of individuals (except in the determination of the

VBGF parameters), which is costly and time-consuming. However, like Hoenig's method and catch-curve analysis, the Beverton-Holt method consistently underestimated Z.

The downward bias of the Beverton-Holt method of estimating Z is produced by sampling variability and the stochastic VBGF used in the operating model. These factors introduced variability in estimates of l_{bar}, the mean length of sampled clams above the MLS (Eqn. 4). Although, for all model scenarios, the mean of the distribution of l_{bar} is not significantly different from the true l_{bar} (t-test, P=0.99, N=1000), the non-linearity of the Beverton-Holt estimator (Majkowski 1982) means that an overestimate of l_{bar} results in an underestimate of Z of a greater magnitude than the overestimate of Z produced by an identical underestimate of l_{bar}.

Although my simulation results indicate that the Beverton-Holt method of estimating Z is relatively insensitive to the sampling methods simulated in this study (Fig. 4), in practice the Beverton-Holt method probably <u>is</u> sensitive to sampling method. This is because although sampling with a lower detection limit (D20) gave biased estimates of the VBGF parameters, the effects of overestimating $L\infty$ and underestimating K were compensatory (see Majkowski 1982). Therefore, estimates of Z from sampling with a lower detection limit were similar to estimates given when representative sampling (RS) was used. Differences between true and simulated recruitment variability, growth variability, sampling variability, sampling methods, and lower detection limit mean that biases of a different magnitude or direction in the VBGF parameter estimates might occur than shown here. Consequently, in practice, sampling method may affect the results of the Beverton-Holt method. Therefore, although using some method to detect small clams increases sampling costs, these costs may be justified by the increase in accuracy of the VBGF parameter estimates and consequently in estimates of Z. However, this is unknown without further information about true conditions (e.g., recruitment variability, mortality rates, etc.) and further simulations to determine the sensitivity of VBGF parameter estimates and the Beverton-Holt method to changes in these conditions.

My results also show that bias in Beverton-Holt estimates increased when, for a given M, fishing mortality increased (and vice versa). Ralston (1989) also found that the Beverton-Holt estimator became more negatively biased as Z increased but this bias was very small (< -3%). However, he used a deterministic VBGF, which may explain why the bias was so small because, unlike the stochastic VBGF used in this study, it will not introduce variability into estimates of l_{bar} or the VBGF parameters. Bias in the Beverton-Holt method due to high rates of mortality can be reduced by increasing sample size (Ralston 1989), which is much less costly than increasing sample size for catch-curve analysis since aging is not required.

In addition to the advantages of the Beverton-Holt method described above, problems with Hoenig's method and catch-curve analysis further indicate that the Beverton-Holt method is most appropriate for butter clam stock assessment. Hoenig's method is based on an empirical relationship between longevity and rate of mortality, using maximum recorded life span as the measure of longevity (Hoenig 1983). There are several problems with Hoenig's method. First, maximum life span may be a poor measure of longevity because measures of maximum life span are strongly affected by initial cohort size and sample size (Hoenig 1983, Promislow 1993). Second, although Hoenig found a significant correlation between annual mortality rate and maximum life span in three taxa (molluscs, fish, and cephalopods) ($r^2 = 0.68$ to 0.78), Krementz et al. (1989) did not find significant correlations for two sets of data each across 16 species of birds ($r^2 = 0.27$ and 0.19). Maximum life span is a function of annual mortality rate and annual rate of increase in mortality rate (i.e., senescence) (Promislow 1993), but Hoenig (1983) and Krementz et al. (1989) attempt to correlate only a constant annual mortality rate with maximum life span. Therefore, unexplained variance in Hoenig's relationship between mortality rate and maximum life span is reason to cautiously interpret and apply his equation. Despite this, Hoenig's method has been used to estimate M or Z for Y/R analyses with no consideration of these factors (with the exception of Defeo 1998). My results (Fig. 3), however, show that Hoenig's method is extremely sensitive to sample size and should therefore be used with extreme caution. A final concern with the specific application of Hoenig's method to butter clams is that it is estimated that butter clams are reliably aged only to about 15 years of age (Quayle and Bourne 1972), but they probably survive to at least 20 years (Bourne 1987b). Therefore, Hoenig's method is probably not appropriate for butter clam stock assessment.

Biases in catch-curve analysis are fairly well documented (Ricker 1975). In this study, catch-curve analysis probably underestimated Z for two major reasons. First, several analytical factors biased the slope of the curve downwards. For example, the number of age-classes used in the linear regression was affected by sample size; at low sample sizes the older age-classes were less likely to be sampled, which decreased the total number of age-classes used in the regression. In addition, abundances of zero or one in the older age classes also biased the slope by flattening the tail of the log-frequency vs. age curve. Second, although catch-curve analysis assumes constant recruitment (Ricker 1975), this assumption is not met by the operating model used in this study. Ricker (1975) states that moderate fluctuations of recruitment do not greatly affect estimated values of Z, but that extreme variation in recruitment (e.g., $\sigma_v = 0.5$ or 0.9) makes catch-curve analysis "practically impossible". Therefore, catch-curve analysis is probably not appropriate for butter clams.

Although the results of the sensitivity analyses described in previous sections are explained by simple intuitive reasoning, few authors consider the effects of sampling biases and the violation of model assumptions when empirically estimating parameters for use in invertebrate stock assessment models. My results show clearly, however, that the effects of sampling biases and violation of assumptions can affect the accuracy and precision of parameter estimates and that ignoring bias and imprecision in parameter estimates can result in sub-optimal management strategies and subsequent loss of fishery yield and value. My results are specific to sampling methods for intertidal clams and using the Beverton-Holt Y/R model to set minimum legal sizes. However, the operating model approach, with extensive sensitivity analyses, can be applied to any fishery, using any parameter estimation models, for any stock assessment model. It should always be done as part of stock assessment (Hilborn and Walters 1992).

Applying results to Seal Island: implications for intertidal clam fishery management

VBGF parameter estimates

Although Seal Island VBGF parameter estimates were variable from year to year (Table 1), my simulation results indicate that such variability, or lack of precision, is unlikely to be a serious problem. This is because the optimal MLS (at a given M and F) resulting from these VBGF parameter estimates does not vary greatly and losses associated with small deviations from the true MLS_{opt} are negligible (<5%, e.g., Fig. 6). Variability in the VBGF parameter estimates might be due to variable sample sizes, sampling error, or non-stationarity. Quayle and Bourne (1972) provide mean length-at-age data for Seal Island butter clams pooled across years and sample sizes which give $L\infty$=97.0 mm and K=0.21. These estimates, from no later than 1972, are within the range of estimates from 1980 – 1995 (Table 1), although they are derived from mean length-at-age data (i.e., mean length of clams in each age-class), which probably gives slightly different estimates than those from all length-at-age data. Therefore, it is likely that VBGF parameters are stationary enough at Seal Island that small yearly differences in estimates of $L\infty$ and K will not result in large losses of fishery yield or value due to a given choice of MLS based on those parameter estimates. Consequently, researchers may not need to re-sample and re-estimate VBGF parameters every year or even every several years.

However, while imprecision of VBGF parameter estimates may not result in large losses, my simulation results show that bias in the VBGF parameter estimates will result in loss. The VBGF parameter estimates for Seal Island (Table 1) are based on data collected using only handsorting of substrate, hence the minimum length detected was variable and ranged between 14 and 38 mm. My results strongly indicate that lack of data for smaller clams will bias VBGF parameter estimates, resulting in losses of Y/R and fishery value. Furthermore, the accuracy of VBGF parameter estimates may be affected by sample size, which also varied greatly among survey years (Table 1). Therefore, the empirical VBGF parameter estimates are likely biased but the magnitude of bias, and therefore the magnitude of loss, is unknown.

Researchers must decide whether to use some method for detecting small clams (to improve accuracy) and what sample size to use (increasing sample size improves precision). Tradeoffs exist between the costs of reducing uncertainty in VBGF parameter estimates and gains obtained by decreasing expected losses in fishery yield and value. For example, removing the lower detection limit of 20 mm reduced expected losses by approximately 7% at high sample sizes (Fig. 6) but sampling time and costs approximately double if some method of detecting small clams is used (e.g., sieving substrate through mesh) (R. Lauzier, 1998, pers. comm). Increasing sample size will also increase sampling costs (mostly due to the costs of aging clams). Clam fishery managers should consider, however, that although using some method to detect very small clams and aging large numbers of clams is costly, accurate estimates of the VBGF parameters will help minimize losses. Furthermore, investing in such an extensive sampling program may pay off in the long run because the VBGF parameters are probably stationary enough to preclude their re-estimation for a number of years.

In addition to considering how often the VBGF parameters are estimated at a particular beach and what sampling design to use, managers also need to consider whether they can use VBGF parameter estimates from one population, such as Seal Island, to set management regulations for other populations in B.C.. This is because butter clam growth is strongly affected by latitudinal gradient (Quayle and Bourne 1972), as well as by oceanographic conditions such as tidal currents (Fraser and Smith 1928). Although VBGF parameter estimates from the same year do not exist for butter clam populations over a wide geographical range, Quayle and Bourne (1972) estimate that while butter clams reach 63 mm (the current MLS) at approximately age five years in Barkley Sound, B.C. (49 ° N), they do not reach this size until age nine years in Prince Rupert, B.C. (54 ° N). Such differences in growth results may result in VBGF parameter estimates that affect the optimal MLS enough to justify estimating VBGF parameters and setting management reference points on a regional or beach-by-beach basis. However, without more detailed information on growth in other butter clam populations, this is uncertain.

A simple benefit-cost analysis can quantify the tradeoff between increasing sampling costs for one year against the decrease in sampling costs due to frequent (e.g., yearly) sampling and gains in fishery value due to more accurate and precise VBGF parameter estimates. To do this, however, not only is better information about sampling costs required, but better information of natural and fishing mortality rates at Seal Island is also required. Furthermore, the amount of decrease in expected loss due to removing a lower detection limit is dependent on the values of both M and F. Accurate estimates of M are also essential to deciding whether to set management strategies on a regional basis, because the optimal MLS is more sensitive to changes in the VBGF parameter values at lower values of M (Vetter 1988).

Estimates of Z

Unlike estimates of VBGF parameters, estimates of M have a large effect on the potential benefits of maximizing Y/R at Seal Island. However, this study only considered methods of estimating total mortality rate, Z. To estimate M or F, it is common practice in fisheries management to use some method of apportioning estimates of Z into its components M and F. However, despite the variability in empirical estimates of Z (Table 1) and because of the inherent biases of the estimation methods themselves, using these estimates to estimate M for the Seal Island butter clam population by relating changes in Z to changes in fishing effort is practically impossible due to lack of precise biomass estimates and catch and effort statistics specific to Seal Island.

While the wide variation between years in empirical estimates of Z is plausible due to variability in environmental conditions and fishery landings, simulation results also suggest various sources of error that need to be considered when interpreting and using estimates of Z from Seal Island. First, increasing recruitment variability affected each of the methods of mortality estimation differently, but the true recruitment variability is unknown. Second, the operating model assumed constant and uniform (across age-classes) mortality. Probably neither of these assumptions is correct. For example, intertidal clam populations can experience massive winter mortalities due to storm or frost damage (Franklin and Pickett 1979, Bower et al. 1986). Third, the operating model assumed that clams were uniformly distributed on the beach, thereby eliminating a source of measurement error. However, Seal Island butter clams are contagiously distributed (as are most intertidal clams) (B. Kingzett and N. Bourne, Department of Fisheries and Oceans, Nanaimo, B.C., 1995, unpublished data). Fourth, although simulation results are based on perfectly aged clams, in practice, under-aging of older individuals typically occurs (Ricker 1969, Tyler et al. 1989). Finally, Ralston (1989) showed that time of year had a significant effect on the Beverton-Holt method if recruitment occurred seasonally, as it does with butter clams. All of these factors can affect the accuracy and precision of the three methods of estimating mortality used in this study.

Despite these limitations, however, some rough estimates of the natural mortality rate of Seal Island butter clams can be drawn from the empirical estimates of Z. With the exception of the 1990 catch-curve estimate ($Z=0.057$), all empirical estimates of Z range between 0.10 and 0.36. Although it is likely that these are underestimates, because at least some fishing occurred in almost every year between 1980 and 1995, it is unlikely that M is > 0.36. Furthermore, estimates using the Beverton-Holt method (the most robust and least biased estimator in simulations) range between 0.12 and 0.26, suggesting that it is extremely unlikely that $M<0.1$ and more likely that $M\geq0.1$. Of course, these estimates provide only a range within which the true value of M <u>might</u> lie. The true natural mortality rate is unknown but its value has extremely important implications for setting management reference points (see below). Clearly, better information about the natural mortality rate is required, but in the mean time, uncertainty in the natural mortality rate as well as other life history parameters suggests applying a precautionary approach (FA0 1995) to setting management reference points for Seal Island.

Management reference points for Seal Island - the precautionary approach

The optimal MLS for Seal Island butter clams depends greatly on values of both M and F (Fig. 11). While rough estimates of M can be derived from empirical estimates of Z (see discussion above), more precise estimates are not possible due to the lack of catch data specific to Seal Island. However, in recent years, target harvest rates for intertidal clams have typically been set between 25% and 50% (R. Webb, 1996, pers. comm.) and because butter clams are not subject to high market demand compared to other clam species, Seal Island butter clam harvest rates may be significantly less than 50%.

Uncertainty in both M and F means that a precautionary approach to setting the MLS is required. The current MLS (63 mm) is too low to maximize Y/R only if $M = 0.1$ or if $M = 0.2$ and harvest rates are greater than ~30%. However, I previously concluded that it is likely that $M \geq 0.1$ (see discussion above). If this is true, and harvest rates are generally lower than 30%, then the current MLS is too high to maximize Y/R. However, although Y/R analyses show what combinations of harvest rate and age-at-entry to the fishery make the most efficient use of a particular cohort (i.e., to prevent growth overfishing), they do not account for the effects of harvesting on the reproductive success of a population (i.e., recruitment overfishing). Therefore, setting management reference points solely on the basis of results of Y/R modeling would be naive. For example, if the optimal MLS is below the size of sexual maturity, the reproductive capability of the stock may be seriously compromised. To prevent this, the MLS for butter clams was raised from

38 mm to 63 mm in 1938 based on data on estimated size-at-maturity from Fraser and Smith (1928) to ensure that clams spawn at least once before entering the fishery. However, over 50 years ago Neave (1944) suggested that the 63 mm MLS was not sufficient to ensure reproductive success in butter clams, since he found that older clams were more fecund than smaller clams. Neave's findings and subsequent work on bet-hedging life history strategies (Stearns 1976) strongly suggest the need for a setting a conservative MLS that may not maximize Y/R but will help preserve stocks.

Uncertainty in M and F mean that setting a sub-optimal MLS (i.e. incurring loss of Y/R) is highly likely, because the MLS may be set either too high or too low to maximize Y/R. Applying the precautionary approach would mean that any error in setting the MLS should occur on the high side (i.e., the MLS should be set too high rather than too low) to reduce the chance of recruitment overfishing. Therefore, even if M is believed to be greater than 0.1 and harvest rates are believed to be low (~25%), clam fishery managers should very carefully consider the risks and consequences of recruitment overfishing before lowering the current MLS.

Several additional factors support the need for a precautionary approach. Historical fishing mortality rates might be underestimated because statistics are kept for landed catches only, and poaching, high-grading, and incidental fishing mortality are not taken into account in landing figures. Poaching and high-grading, which are known to occur in B.C. intertidal clam fisheries (R. Webb, 1998, pers. comm.), are difficult to prevent because harvested beaches are widely distributed and distant from landing locations. Incidental fishing mortality is also difficult to prevent due to the nature of clam harvesting, in which a three- or four-tined fork is used to dig substrate and consequently, clam shells are often cracked or broken (these clams are not harvested and will not survive). These factors also result in imperfect control of future harvest rates (i.e., implementation error). Obviously, if the objective of maximizing Y/R is used to set the MLS with an assumed F that is less than the true F because of these factors, loss of fishery yield and value will occur because the MLS will be set too low. Applying a precautionary approach means that for Seal Island, perhaps some arbitrary safety margin should be added to the MLS to account for an unknown magnitude of poaching and incidental fishing mortality. With better information about poaching and incidental mortality, more accurate harvest rates would reduce the need for this safety margin.

Furthermore, in populations for which recruitment is highly variable and seemingly independent of spawner abundances, Y/R models cannot be used to make long-term forecasts of yield since the sizes of future year classes are unknown. Because butter clam recruitment is highly variable, fishery managers and harvesters must further consider whether they prefer periodic, single years of large harvests (i.e., high harvest rate after a large recruitment event) or smaller but more consistent yearly harvests (i.e., sustaining a large recruitment event over several years until the next large recruitment event). This will influence their decisions about setting management strategies such as the MLS, as well as area and seasonal closures. Obviously, clarifying management objectives will also greatly assist managers in setting precautionary management reference points.

Finally, my estimates of loss of fishery value (Fig. 7, 8, 9, 10) may be minimum estimates, meaning that setting a sub-optimal MLS may result in even greater losses than are indicated by simulation results. This conclusion is because these results were based on the assumption that M=0.2 and F=0.3. If these values of M and F are true, then the 1998 Seal Island fishery was close to maximizing Y/R because this combination of M and F give an optimal MLS just one mm less than the current MLS (63 mm). However, if my assumption of M=0.2 is actually an underestimate of the true value of M, losses will be even greater (due to the asymmetric expected loss curve, Fig. 8). This further supports the need for precautionary management, as well as the need for benefit-cost analyses to determine the most cost-effective sampling program.

Managers should carefully consider their management objectives, the possibility of losses of yield or value due to setting management reference points based on uncertain parameter estimates, as well as shortcomings of the stock assessment models used in management planning before setting management reference points. Until more information about butter clam mortality and recruitment is available, the current MLS of 63 mm for the Seal Island butter clam fishery should not be lowered. This will probably not result in large losses of yield or value since the current MLS is fairly close to the optimal MLS suggested if M ≥0.2 and harvest rates are not typically high (i.e., F≤0.7). However, managers should consider raising the current MLS, especially if future harvest rates increase above current levels, because the current MLS may not adequately protect the spawning population.

Clearly, Y/R analyses should not be the culmination of stock assessment nor the sole source of management advice, especially with the recent shift in fisheries management from objectives of maximizing or optimizing biological or economic yield to precautionary objectives such as prevention of low spawner abundances (Caddy and Mahon 1995). However, Y/R modeling is a useful tool in data-limited fisheries provided its shortcomings are recognized. Furthermore, I have incorporated the Y/R model into a framework for assessing the implications of different sampling methods and sample sizes, different parameter estimation methods, and varying levels of recruitment on the stock assessment model output.

While authors sometimes acknowledge uncertainty in estimates of parameters they use in stock assessment models, few consider the management implications of "controllable" sources of error such as sampling designs and methods of estimating input parameters. Management decisions based on the results of stock assessment models parameterized with biased input parameters will result in sub-optimal management regulations. Applying this type of framework <u>before</u> implementing management regulations can improve fishery management by allowing researchers to identify tradeoffs between investment in data collection and gains in fishery yield and value, as well as what information gaps exist and which are most important to fill.

Data collection by user groups

My results show how sampling method, sample size, and method of parameter estimation can affect the accuracy and precision of parameters used in quantitative fisheries stock assessment. However, accuracy and precision can be affected not only by how data are collected but also by whom data are collected. Shared responsibility between government agencies and user groups for data collection and analysis is a key aspect of many successfully co-managed fisheries (Pinkerton 1989, Pinkerton and Weinstein 1995), but it can present several challenges for fisheries stock assessment. However, it also presents unique opportunities for data collection which can improve stock assessment.

My results show that tradeoffs exist between the costs of reducing uncertainty in parameter estimates and gains in fishery yield and value realized by improving the accuracy and precision of parameter estimates. However, government budget cutbacks and limited staff availability may mean that funds for reducing uncertainty by, for example, increasing sample sizes and using some method for detecting small clams, are simply unavailable. Involving user groups in data collection can help overcome these constraints in several ways.

First, existing costs or costs of new data collection can be borne in part by user groups. In addition, communities and harvesters also often pursue alternative sources of expertise and funding from, for example, academic institutions or non-governmental organizations. New Jersey clam harvesters greatly improved data collection and analysis for a clam fishery by involving local community members, academics, and non-government scientists (McCay 1989). Such funding and expertise, when combined with existing government resources, can reduce uncertainty in parameter estimates used in B.C. clam fishery management by making it possible to undertake data collection that was previously infeasible due to lack of funding or staff. For example, with existing government resources, intensive sampling to accurately and precisely estimate growth parameters of a clam population might be possible every ten years, but with additional resources contributed by user groups, sampling might occur more frequently.

Second, data collection by user groups can be less costly than collection of the same data by government agencies. Data are not often collected where government agencies are located, so travel and accommodation expenses are incurred when government agencies are responsible for data collection. These expenses can be greatly reduced or absent when data are collected by local community members. For example, it was cheaper for the Alaska Department of Fish and Game (ADFG) to hire a Yup'ik (Eskimo) fisherman who lived near the Kuskokwim River mouth to record and submit daily fish counts from a nearby test fishery than it would have been for ADFG staff accommodation for the 70-day fishery (Pinkerton and Weinstein 1995). Reducing data collection costs has important implications for intertidal clam fishery management in British Columbia for reasons such as the wide geographical range of harvested beaches. If differences in somatic growth between populations are significant enough to justify regional management strategies, it would be extremely costly for the DFO to collect data from beaches along the B.C. coast. Using morphological data collected by local communities to estimate growth parameters could greatly decrease sampling costs. Furthermore, my results showed that accurate estimates of F are required to accurately estimate M and reduce possible losses of yield and value. Local user groups could assume responsibility for reporting catches, making beach-specific catch statistics possible and thereby reducing uncertainty in estimates of F and M. It would be in the long-term interests of users to help DFO obtain better estimates of those parameters and the resulting optimal management regulation.

Third, although some types of data might not be collected simply due to budget and staff constraints, local harvesters and community members often have different data or more extensive knowledge of local stocks than government biologists. Examples of such data are knowledge of historical environmental events that affect clam abundances or recruitment, or knowledge of locations of large aggregations of clams. This knowledge often enables harvesters and community members to construct hypotheses about events that government biologists and managers cannot. This knowledge can improve stock assessment by filling information gaps identified by government biologists as well as identifying directions for future research. Furthermore, local knowledge can further reduce data collection costs because harvesters and community members are often familiar enough with local areas to help government biologists quickly determine which beaches and where on particular beaches to sample as well as the best way of traveling to those beaches.

However, several technical issues concerning data quality arise with the involvement of user groups in data collection. Data collection requires expertise on statistical sampling methods. If user groups are involved in data collection, this expertise must be developed locally or sought elsewhere. User groups may choose to hire or consult with a fisheries biologist or statistician (e.g., Jones et al. 1998), or obtain training from government stock assessment biologists. In either case, careful planning before data are collected and careful implementation of sampling design will reduce statistical and sampling errors which can bias parameter estimates.

Sampling errors can also result from poor technique during sampling. In particular, intertidal clam sampling requires certain degree of precision and care in laying transects, digging plots, and taking morphological measurements. Reliable, committed individuals are required to do this. However, this is unlikely to be problematic if user groups have already shown willingness to contribute financially or participate in co-management initiatives. For example, before any co-management agreements between the Council of the Haida Nation (CHN) and the Department of Fisheries and Oceans were in place, the CHN stated that one of their objectives was "to develop technical, biological, and resource management skills of our people in order that we might develop effective fisheries management programs in the future" (Richardson and Green 1989).

However, the benefits of shared data collection responsibilities are seriously compromised if government agencies do not trust the quality of data they receive from user groups or if they do not trust the person(s) collecting data. Mutual trust and confidence in data can be established in several ways. First, government agencies can investigate the work history and reliability of individuals who will collect data. For example, the particular Yup'ik fisherman hired by the ADFG to record test fishery counts was considered well known and trusted after an initial period of co-operation in the test fishery (Pinkerton and Weinstein 1995). Second, government employees can work alongside the individuals initially and observe their personalities and work habits. In the case of the Yup'ik fisherman, an ADFG technician worked with the fisherman for several months to ensure that he and his methods were reliable (D. Senecal-Albrecht, Bering Sea Fishermen's Association, Anchorage, Alaska, 1998, pers. comm.). Third, government employees can verify the accuracy of data by performing "checks". The ADFG technician found that catch numbers reported by the Yup'ik fisherman correlated well with other indicators of fish entry into the Kuskokwim River (D. Senecal-Albrecht, 1998, pers. comm.). In many cases of shared responsibility for data collection, mutual trust, respect, and confidence in data has been established in less than a year.

Another example of successful shared responsibility for data collection is the Gitksan sockeye salmon (*Onchorhynchus nerka*) fishery on the upper Skeena River, B.C. Under an Aboriginal Fisheries Strategy (AFS) agreement with DFO, the Gitksan are responsible for spawning escapement surveys, fish habitat assessment, and monitoring programs (Pinkerton and Weinstein 1995). In-season, the Gitksan and DFO both collect data on stock timing, abundance, and composition and exchange information through weekly telephone conference calls. Previous to the AFS agreement, the Gitksan opposed the presence of DFO fisheries officers in their territory and resisted DFO involvement in data collection. Since the implementation of the agreement, however, the relationship between the Gitksan and DFO has improved significantly. The Gitksan and DFO are usually able to agree on interpretation of the data, and they are now working co-operatively to reduce the probability of overfishing of smaller, less productive stocks through better stock-by-stock management, selective fishing, and lower harvest rates (Pinkerton and Weinstein 1995).

Besides the potential benefits described above, shared responsibility for data collection between government agencies and user groups can increase the success of co-managed fisheries in several ways. Sharing responsibilities acknowledges the existence of human capital, or the knowledge, skills, experiences, attitudes, and values about problem-solving that communities build up over time (Pinkerton and Weinstein 1995). Consequently, the development of mutual trust and respect can result in increased credibility of government managers with harvesters and vice versa. For example, management decisions based on the analysis of data collected co-operatively are often more "believable" to local harvesters (Pinkerton 1989). Similarly, user groups who are willing to participate in and bear costs of stock assessment often have more influence and ability to exert pressure on government agencies (McCay 1989, Pinkerton 1989). Involvement of user groups often fosters a sense of stewardship in harvesters and local communities, leading to increased compliance with regulations and therefore decreased costs of enforcement (Pinkerton and Weinstein 1995).

The operating model approach I used in this study allowed me to quantify how different sampling methods affected the accuracy and precision of parameter estimates used in clam stock assessment. In addition, it allowed me to identify where more information is required to reduce potential losses (e.g., natural mortality rate) as well as tradeoffs between collecting data to reduce uncertainty in parameter estimates and reducing losses in fishery yield and value. This information is valuable not only to government biologists but also to user groups participating in co-managed fisheries. By seeking technical expertise through the co-operation of government agencies or consultation of non-government biologists, user groups can also use this simple approach to improve management of local clam resources. Furthermore, they can improve the approach by developing innovative and cost-effective solutions to traditional government constraints, allowing more accurate and precise estimation of parameters used in stock assessment and consequently better management of clam resources.

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Table 1. Empirical parameter estimates for Seal Island butter clam surveys.

Survey year	1981	1982	1990	1992	1995
Sample size	1029	208	100	360	713
Minimum length detected (mm.)	14	38	21	15	17
von Bertalanffy growth function parameter estimates*					
L_∞ (mm)	93.13	99.04	119.04	98.48	**102.16**
K	0.242	0.167	0.109	0.163	**0.183**
t_0 (yr)	0.345	1.193	0.915	0.549	**0.216**
Optimal MLS (mm) (M=0.2, F=0.3)	61	59	61	58	62
Estimates of total instantaneous mortality, Z					
Catch curve	0.28	0.32	0.057	0.10	0.16
Beverton-Holt	0.24	0.26	0.19	0.12	0.16
Hoenig	0.30	0.36	0.32	0.24	0.30

* VBGF parameter estimates in bold (1995) were used in operating model

Figure 1. Generalized flow chart of simulation model components and calculation of expected loss.

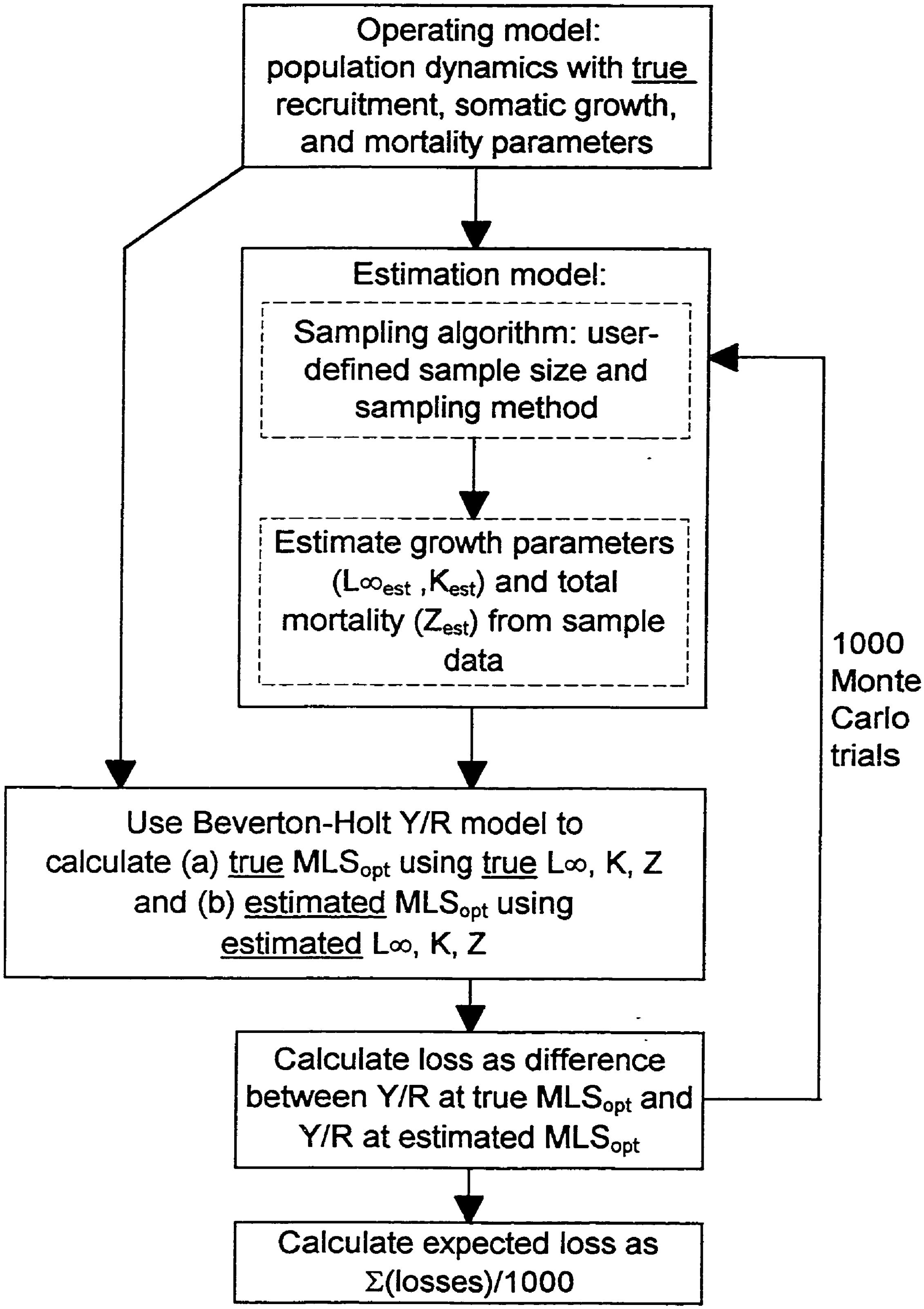

Operating model:
population dynamics with true recruitment, somatic growth, and mortality parameters
Estimation model:
Sampling algorithm: user-defined sample size and sampling method
Estimate growth parameters ($L\infty_{est}$,K_{est}) and total mortality (Z_{est}) from sample data
1000 Monte Carlo trials
Use Beverton-Holt Y/R model to calculate (a) true MLS_{opt} using true $L\infty$, K, Z and (b) estimated MLS_{opt} using estimated $L\infty$, K, Z
Calculate loss as difference between Y/R at true MLS_{opt} and Y/R at estimated MLS_{opt}
Calculate expected loss as Σ(losses)/1000

Figure 2. Effect of sample size and sampling design on accuracy and precision of estimates of (A) asymptotic length, $L\infty$, and (B) the Brody growth coefficient, K (σ_v=0.9 (Eqn. 1), M=0.2, F=0.3). Sampling designs: RS, representative sampling; D20, lower detection limit 20 mm; X, extra clams in oldest age classes (see text for further description). Error bars represent 95% confidence intervals. Dotted horizontal lines indicate true value of parameters ($L\infty$=102.16, K=0.1825).

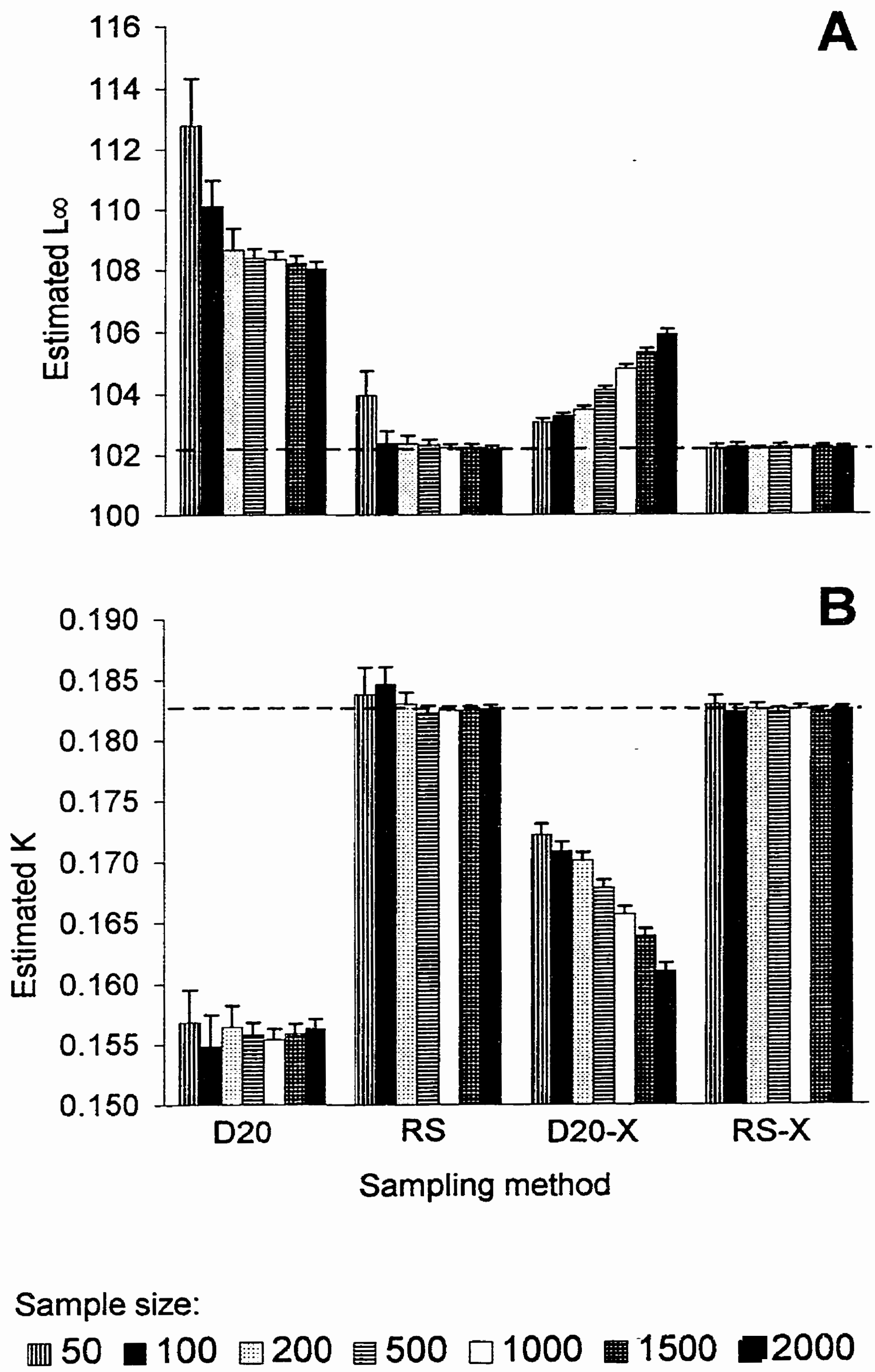
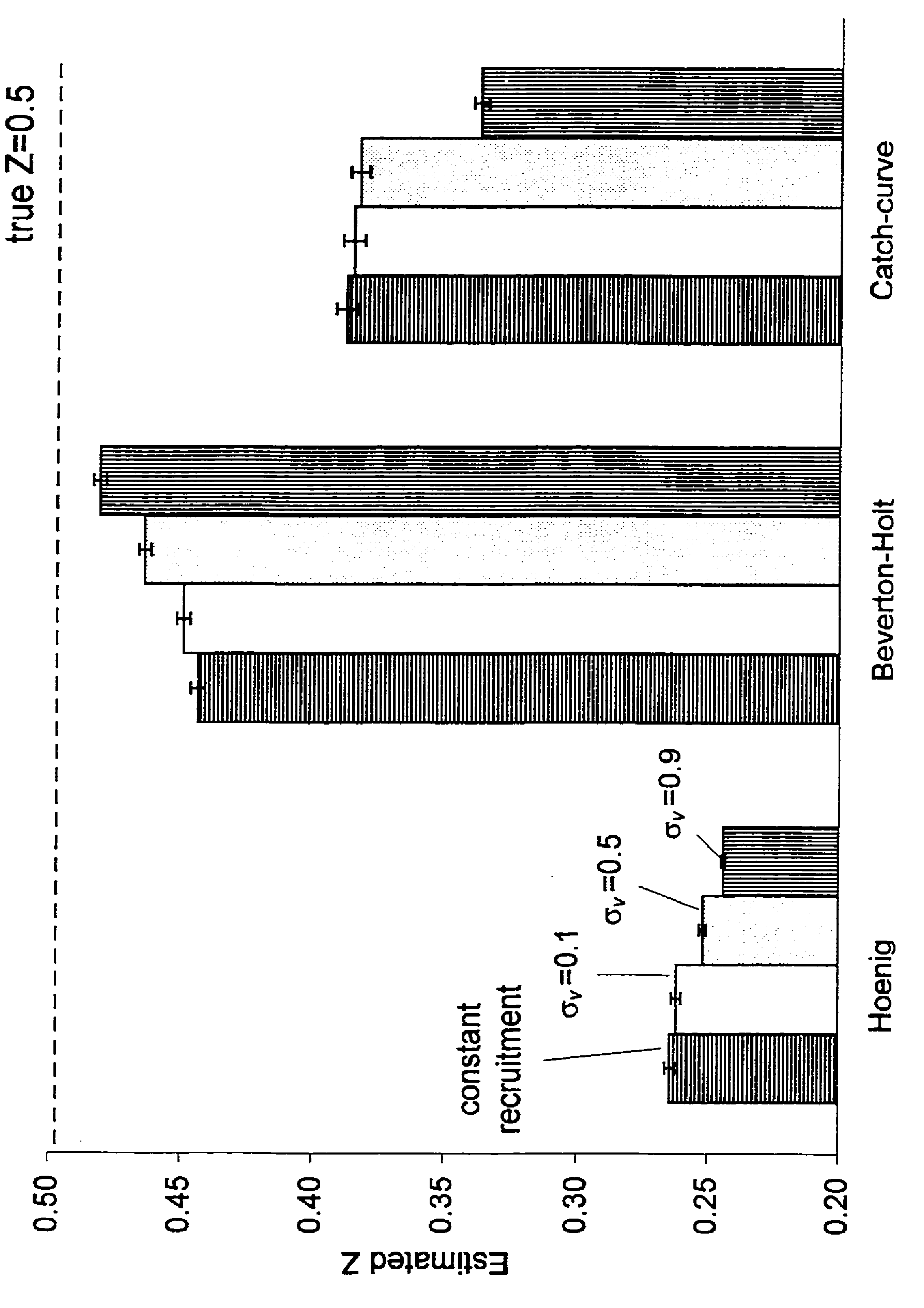

A
116
114
112
110
108
106
104
102
100
Estimated L∞
B
0.190
0.185
0.180
0.175
0.170
0.165
0.160
0.155
0.150
Estimated K
D20
RS
D20-X
RS-X
Sampling method
Sample size:
50
100
200
500
1000
1500
2000

Figure 3. Effect of level of recruitment variability (σ_v, Eqn. 1) on accuracy and precision of estimates of total instantaneous mortality, Z, using three methods of estimating Z (representative sampling, sample size = 500, M=0.2, F=0.3). Error bars represent 95% confidence intervals. Dotted horizontal line indicates true value of Z (0.5).



true Z=0.5
Estimated Z
0.50
0.45
0.40
0.35
0.30
0.25
0.20
constant recruitment
σ_v=0.1
σ_v=0.5
σ_v=0.9
Hoenig
Beverton-Holt
Catch-curve

Figure 4. Effect of sample size and sampling method on accuracy and precision of estimates of total instantaneous mortality, Z, using three methods of estimating Z (σ_v=0.9 (Eqn. 1), M=0.2, F=0.3). Sampling designs: RS, representative sampling; D20, lower detection limit 20 mm). Error bars represent 95% confidence intervals. Dotted horizontal line indicates true value of Z (0.5).

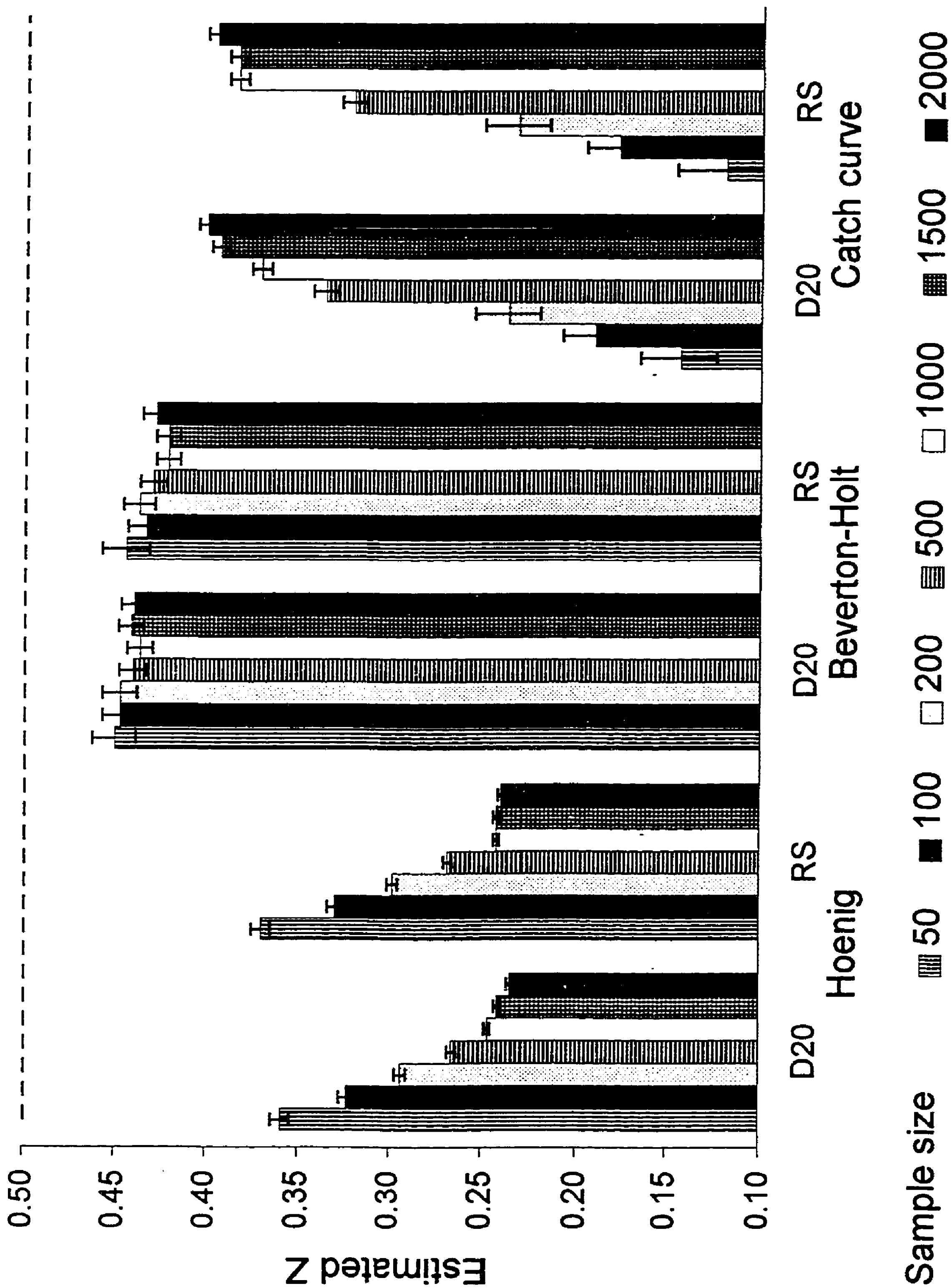

Estimated Z
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
Sample size
D20
RS
Hoenig
D20
RS
Beverton-Holt
D20
RS
Catch curve
50
100
200
500
1000
1500
2000

Figure 5. Effect of level of (A) instantaneous natural mortality, M, for F=0.3, and (B) instantaneous fishing mortality, F, for M=0.2, on the accuracy and precision of estimates of total instantaneous mortality, Z (σ_v=0.9 (Eqn. 1), representative sampling (RS), sample size = 500). Error bars represent 95% confidence intervals.

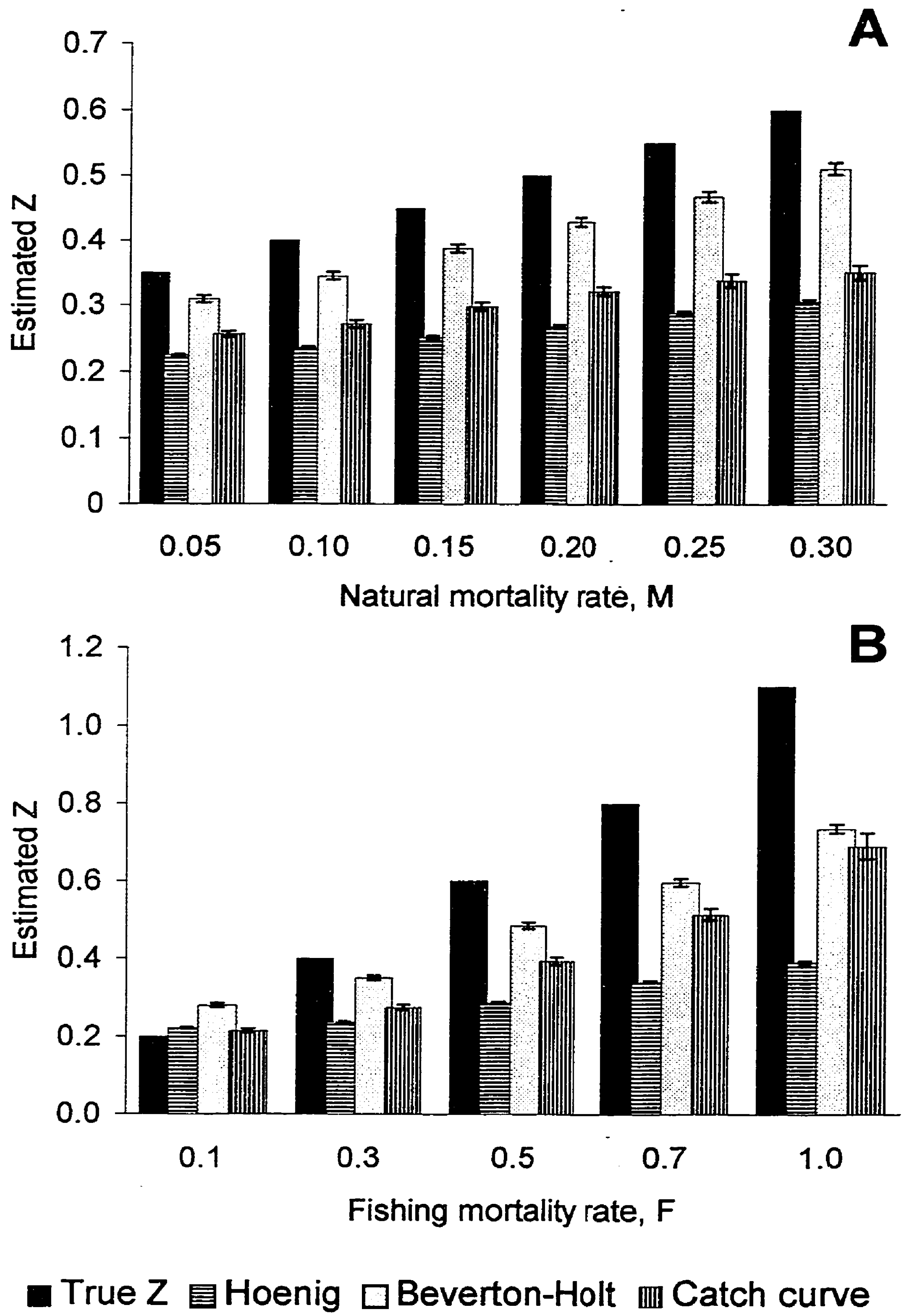

A
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Estimated Z
0.05
0.10
0.15
0.20
0.25
0.30
Natural mortality rate, M
B
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Estimated Z
0.1
0.3
0.5
0.7
1.0
Fishing mortality rate, F
True Z
Hoenig
Beverton-Holt
Catch curve

Figure 6. Expected loss calculation. Bars show distribution of 1000 estimated optimal MLSs (σ_v=0.9 (Eqn. 1), F=0.3, representative sampling (RS), sample size = 500) when the true level of natural mortality (M=0.2) is known (light bars) and when M is underestimated as 0.1 (solid bars). Solid line indicates loss of Y/R; loss = 0 when the estimated MLS_{opt} = the true MLS_{opt} = 62 mm.

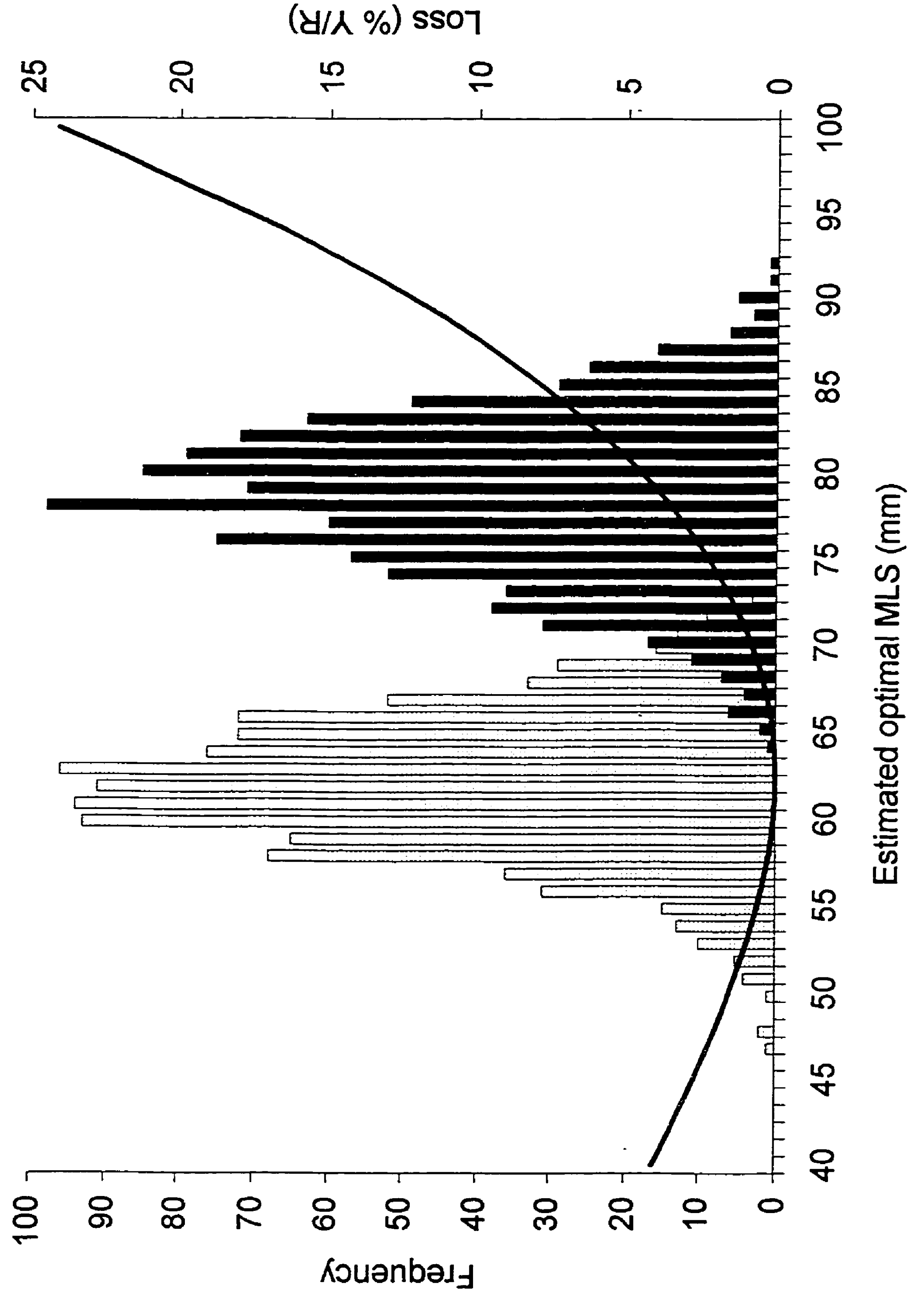

Loss (% Y/R)
25
20
15
10
5
0
100
90
80
70
60
50
40
30
20
10
0
Frequency
40
45
50
55
60
65
70
75
80
85
90
95
100
Estimated optimal MLS (mm)

Figure 7. Expected loss of percent Y/R and Seal Island fishery value due to uncertainty in VBGF parameters, at different sample sizes ((σ_v=0.9 (Eqn. 1), M=0.2, F=0.3). Sampling designs: RS, representative sampling; D20, lower detection limit 20 mm; X, extra clams in oldest age classes (see text for further description).

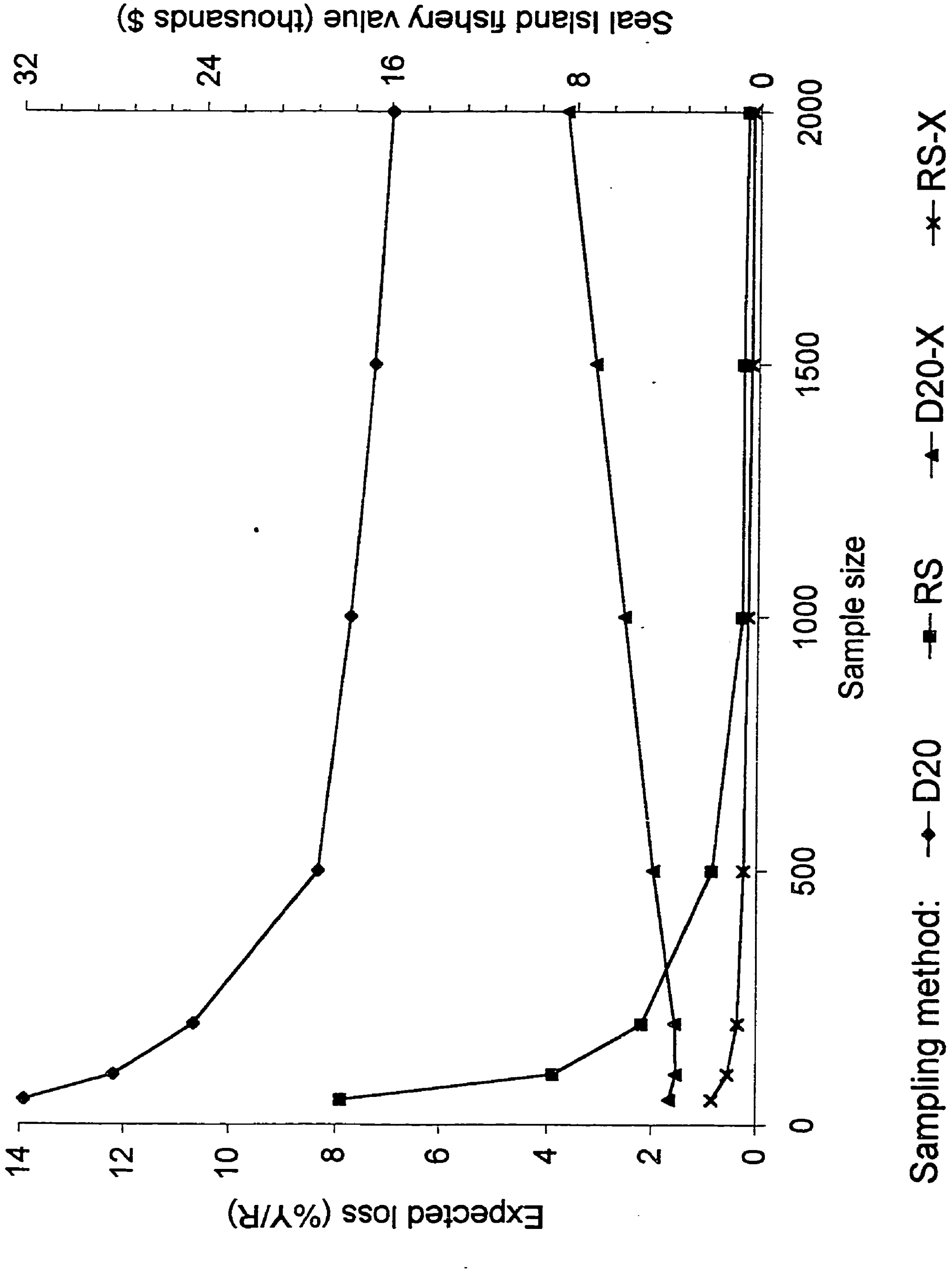

Expected loss (%Y/R)
Seal Island fishery value (thousands $)
Sample size
Sampling method:
D20
RS
D20-X
RS-X
0
2
4
6
8
10
12
14
500
1000
1500
2000
16
24
32

Figure 8. Expected loss of percent Y/R and Seal Island fishery value due to uncertainty in VBGF parameters as well as inaccurate estimates of natural mortality, M (σ_v=0.9 (Eqn. 1), true M=0.2, F=0.3, sample size = 500). Sampling designs: RS, representative sampling; D20, lower detection limit 20 mm; X, extra clams in oldest age classes (see text for further description).

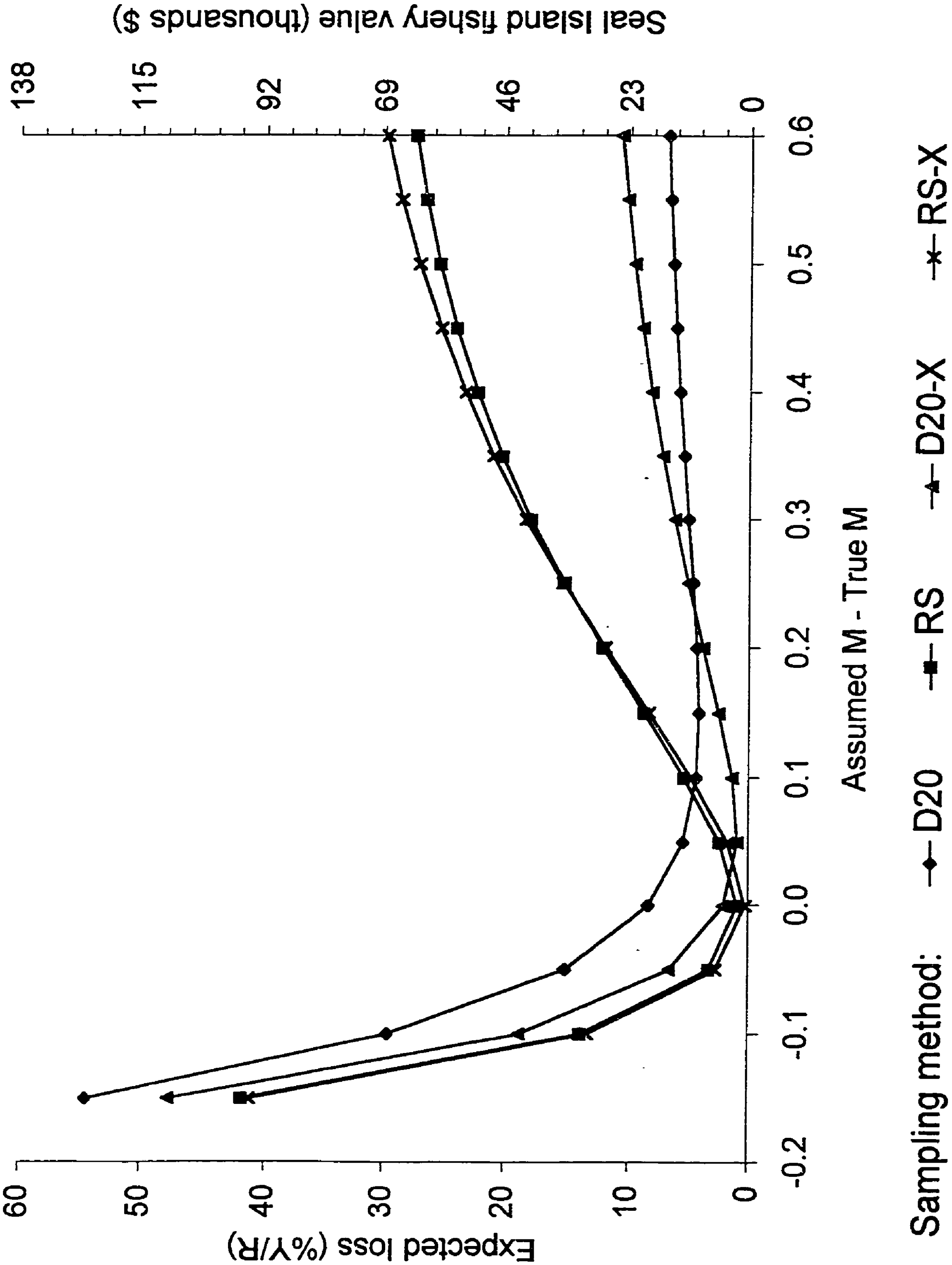

Seal Island fishery value (thousands $)
138
115
92
69
46
23
0
Expected loss (%Y/R)
60
50
40
30
20
10
0
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Assumed M - True M
Sampling method:
D20
RS
D20-X
RS-X

Figure 9. Effect of sample size on expected loss of percent Y/R and Seal Island fishery value due to uncertainty in VBGF parameters and inaccurate estimates of natural mortality, M, using (A) a lower detection limit of 20 mm (D20) and (B) representative sampling (RS) (σ_v=0.9 (Eqn. 1), true M=0.2, F=0.3).

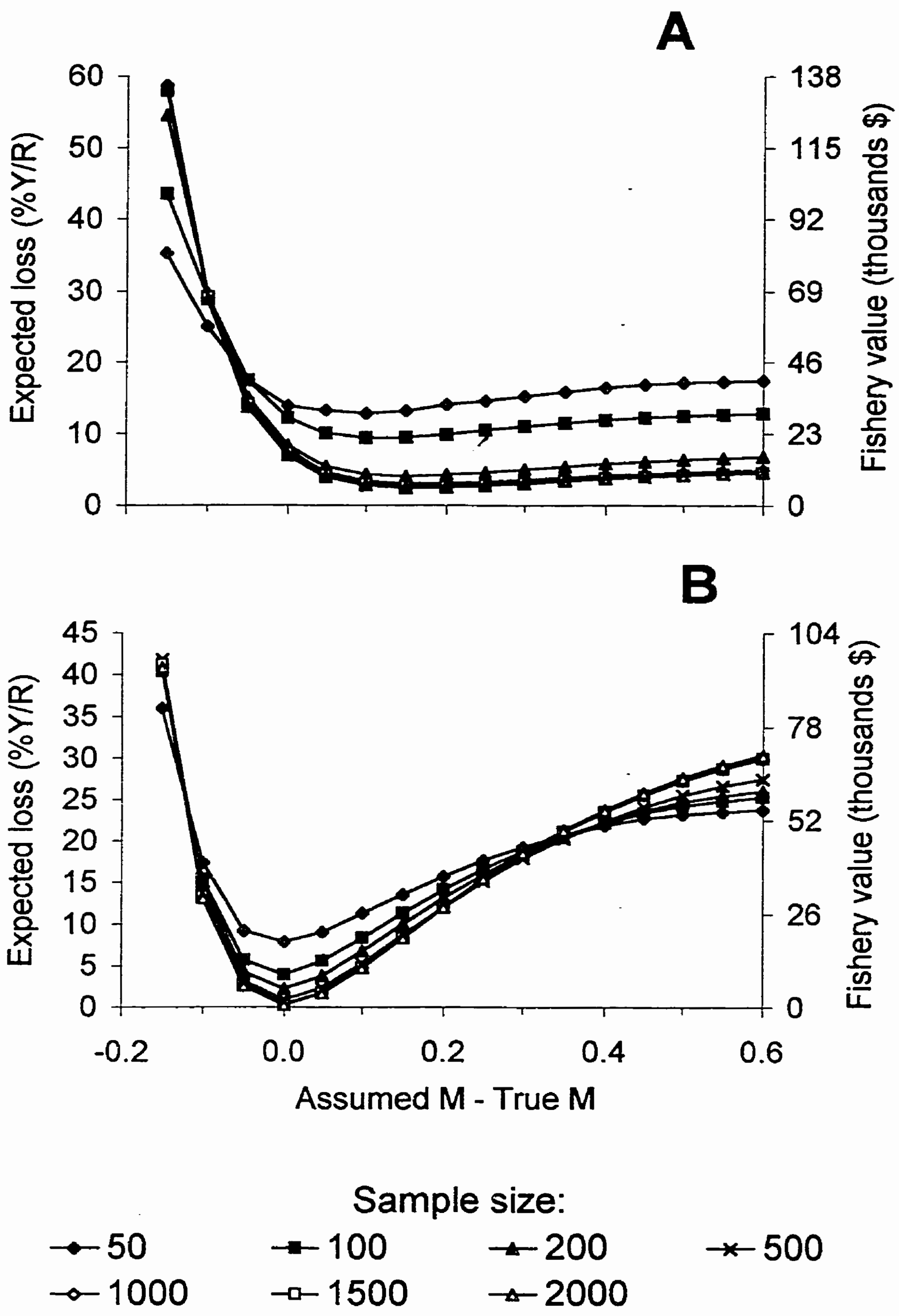
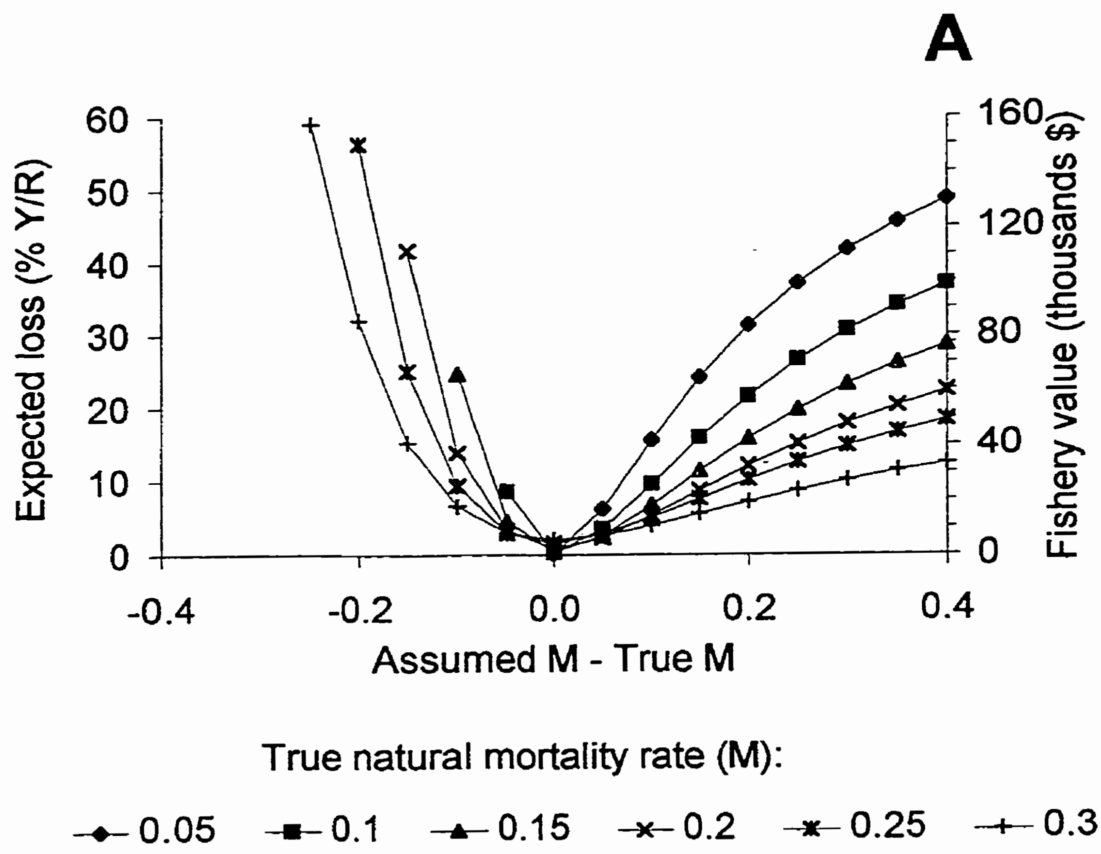

A
Expected loss (%Y/R)
0
10
20
30
40
50
60
Fishery value (thousands $)
0
23
46
69
92
115
138
B
Expected loss (%Y/R)
0
5
10
15
20
25
30
35
40
45
Fishery value (thousands $)
0
26
52
78
104
-0.2
0.0
0.2
0.4
0.6
Assumed M - True M
Sample size:
50
100
200
500
1000
1500
2000

Figure 10. Effect of (A) instantaneous natural mortality, M, and (B) instantaneous fishing mortality, F, on expected loss of percent Y/R and Seal Island fishery value due to uncertainty in VBGF parameters and inaccurate estimates of M. (A) constant F=0.3 (B) constant M=0.2 (σ_v=0.9 (Eqn. 1), representative sampling (RS), sample size = 500).


A
60
50
40
30
20
10
0
160
120
80
40
0
Expected loss (% Y/R)
Fishery value (thousands $)
-0.4
-0.2
0.0
0.2
0.4
Assumed M - True M
True natural mortality rate (M):
0.05
0.1
0.15
0.2
0.25
0.3

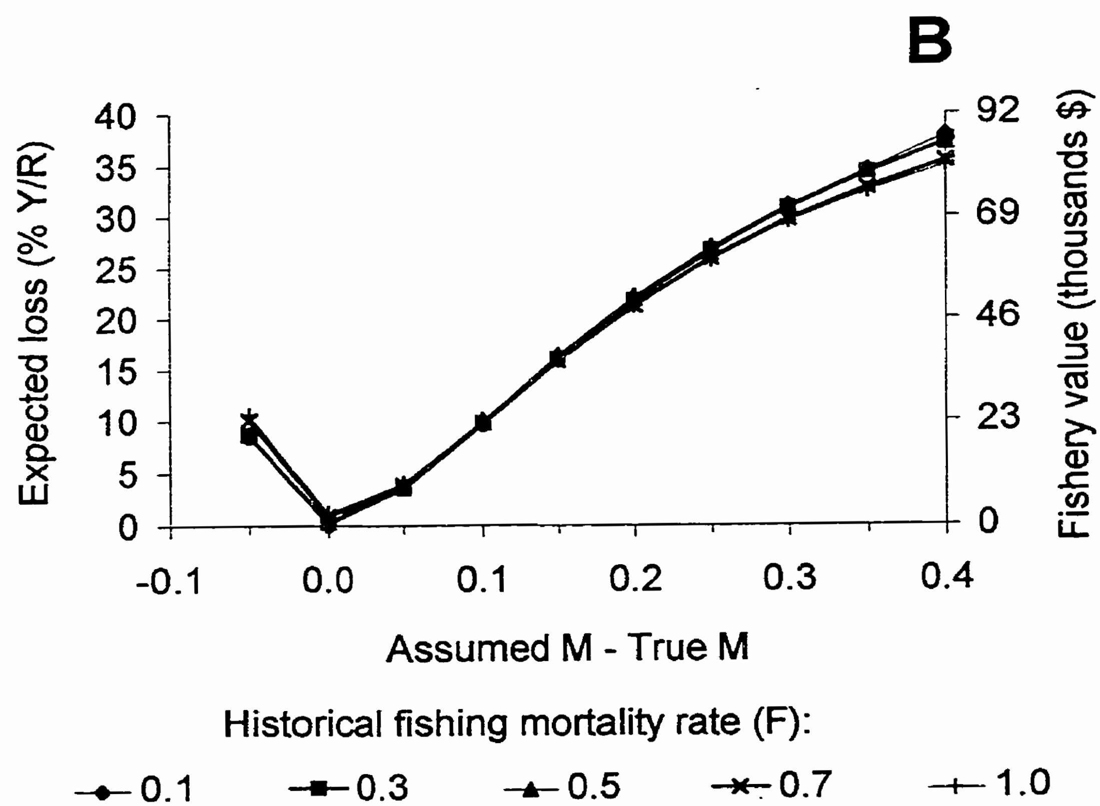
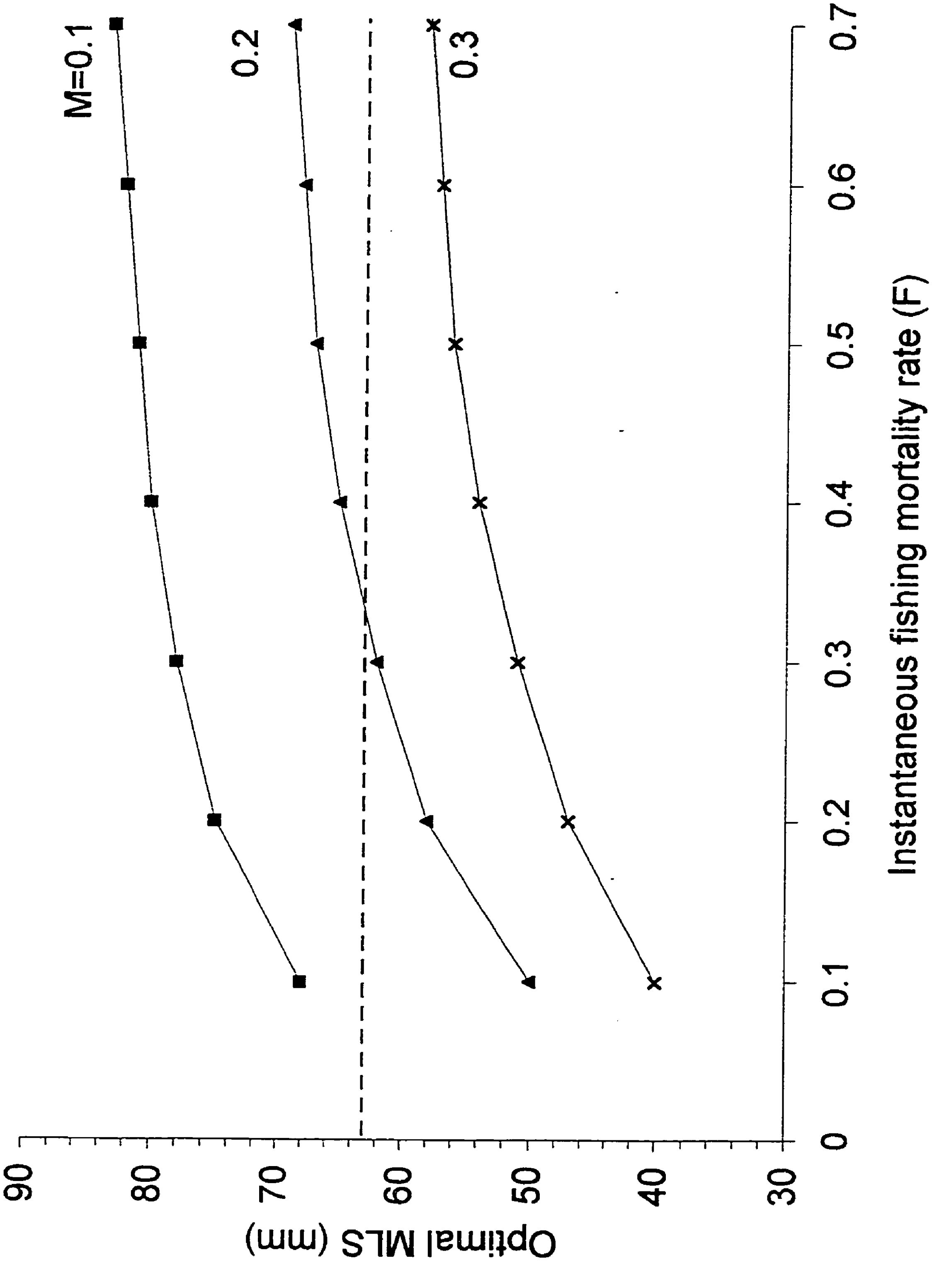
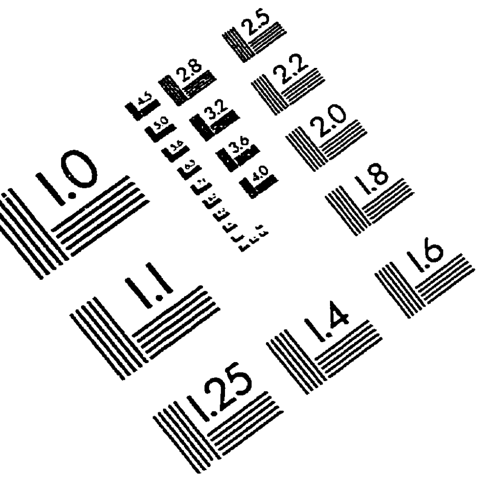

B
40
35
30
25
20
15
10
5
0
92
69
46
23
0
Expected loss (% Y/R)
Fishery value (thousands $)
-0.1
0.0
0.1
0.2
0.3
0.4
Assumed M - True M
Historical fishing mortality rate (F):
0.1
0.3
0.5
0.7
1.0

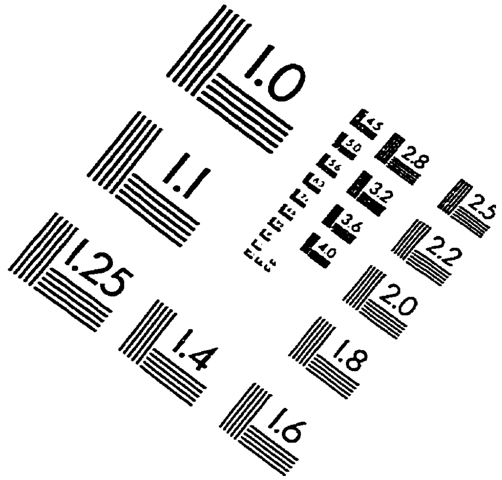
Figure 11. Optimal MLS (the MLS that maximizes Y/R at a given M and F) at different levels of M and F. Dotted line indicates the current MLS of 63 mm.

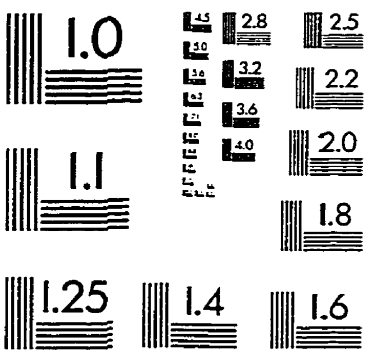


Optimal MLS (mm)
90
80
70
60
50
40
30
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Instantaneous fishing mortality rate (F)
M=0.1
0.2
0.3

IMAGE EVALUATION TEST TARGET (QA-3)

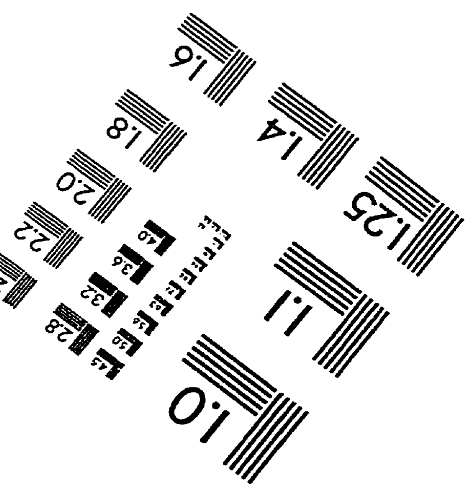


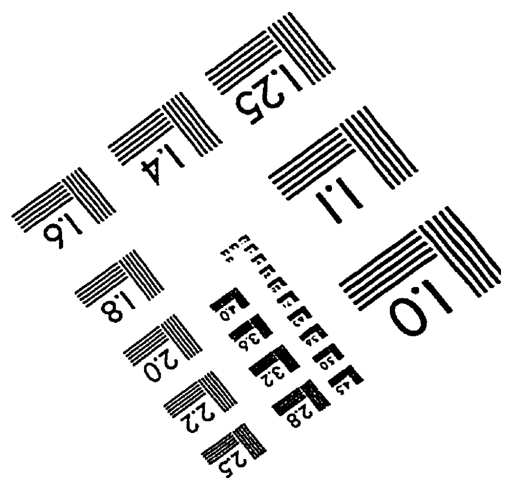




150mm

6"





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