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Estimating reference fishing mortality rates from noisy spawner-recruit data

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Abstract

We review and evaluate methods of estimating reference fishing mortality rates from spawner-recruit (SR) data to obtain maximum sustainable yield. Using Monte Carlo simulations, we found that a reference fishing mortality rate derived from the maximum likelihood estimates of the SR parameters was less biased than reference fishing mortality rates obtained using the mode of the marginal probability distribution for the maximum rate that spawners produce recruits or by finding the fishing mortality rate that maximizes the expected yield. However, the maximum likelihood method produced the most variable estimates, at times leading to substantial under- or over-exploitation of the population. In contrast, the decision theoretic method of maximizing the expected yield exhibited less variability, produced higher yields and substantially reduced the risk of over-exploiting the population. We show how these methods can be extended to include information from other populations. Bayesian priors for the SR parameters, obtained through meta-analyses of population dynamics at some higher organizational level (e.g., the species), may be used to assess the plausibility of parameter estimates obtained for a single population, or combined with the data for the population of interest. Reference fishing mortality rates are then estimated from the resulting joint posterior distribution.

Keywords: Bayesian, decision theory, fisheries management, meta-analysis, alewife (*Alosa pseudoharengus*)

Introduction

Biological reference points (BRP's) are indices based on the biological characteristics of a fish stock and the characteristics of its fishery. They are used to gauge whether specific management objectives are being achieved, provide both the link between stock assessment and management objectives (Caddy and Mahon 1995) and a basis for risk analysis of management actions (Punt and Hilborn 1997). As the use of biological reference points becomes more prevalent in fisheries management, assessment of the precision of BRP estimates and development of methods that incorporate uncertainty into BRP estimation become more crucial (Caddy and McGarvey 1996; Overholtz 1999; Richards and Maguire 1998).

The most important source of uncertainty in estimating the long-term productivity of a fishery is the degree of density-dependence in the spawner-recruit (SR) relationship (Getz et al. 1987; Myers et al. 1999). However, many SR data sets contain only limited information about SR parameters for the population of interest (Myers et al. 1999). When estimated using only data from an individual population, SR parameter estimates are at times biologically implausible (e.g., estimates of the maximum rate at which spawners produce recruits that are infinite), or are poorly determined (Barrowman and Myers 2000; Gibson and Myers 2003a), particularly when there is little contrast in the SR data. Despite this uncertainty, the maximum likelihood estimates (MLE) of the SR parameters are often taken to be the "best" estimates and used to calculate the fishing mortality rate that produces maximum sustainable yield (F_{msy}).

Several methods have been proposed to deal with uncertainty in the SR relationship, including alternative reference points that do not explicitly include an SR component, methods that do not require specification of the functional form of the SR model and methods that explicitly include uncertainty in the SR parameter estimates or model choice. For example, the reference fishing mortality rate $F_{x\%}$ is the fishing mortality rate that reduces the spawning biomass per recruit (SPR) to x% its unfished level (Goodyear 1977; Shepherd 1982). This reference point is based on the premise of protecting spawning biomass, but does not require an SR relationship for its estimation. However, the selection of an appropriate value for x is problematic, and may be obtained only with reference to the productivity of the population (or other populations) or based on experience (Mace and Sissenwine 1993; Mace 1994; Clark 2002). Similarly, reference points based on yield per recruit (YPR) analyses (Beverton and Holt 1957) may also require adjustment based on stock productivity. An example is the adoption of $F_{0.1}$ (Gulland and Boerema 1973) when experience with F_{max} suggested that it advocated fishing mortality rates that exceeded the rates that would produce maximum sustainable yield.

Bayesian and decision theoretic methods have been used to explicitly include parameter uncertainty in the reference point estimation framework. Clark (1991) suggested that a production-based reference fishing mortality rate could be estimated without knowledge of the true SR model by finding the fishing mortality rate that maximizes the minimum yield (F_{mmy}) over two SR models and a range of model parameters. Ianelli and Heifetz (1995) integrated over the likelihood surface for two SR parameters to obtain the marginal probability density for the slope at the origin of the SR relationship. Ianelli and Heifetz do not directly calculate a reference F from the marginal probability density for the slope at the origin, although their method does directly incorporate uncertainty in this parameter into their risk assessment. Chen and Holtby (2002) used the marginal probability density for the SR slope at the origin to estimate the probability density for F_{msy}. This approach has the advantage that uncertainty in the half saturation constant is explicitly included and that the marginal probability density for α can be used to assess the precision of the resulting reference *F*. Its disadvantage is that all possible values of the SR parameters are considered equally favourable. If some points in the SR parameter space produce equilibrium yields at MSY that are higher than at other points, these points may be considered more favourable. A decision theoretic approach to estimating a reference point combines the probability for the model parameters with management objective criteria such as maximizing yield (Frederick and Peterman 1995). Brodziak (2002) used a decision theoretic approach to estimate a reference *F* that maximizes the expectation of the yield over two SR models (the Ricker and Beverton-Holt) and three values of a shape parameter for each model. This reference point, $F_{\mathrm{maxE[Y]}}$, includes uncertainty in the SR parameters, uncertainty in model selection as well as the consequences of adopting a reference *F* in its estimation.

A major problem with reference point estimation based on SR analyses is that the long SR time series spanning a range of stock sizes required for the analyses are simply unavailable for many populations (Caddy and Mahon 1995). Drawing upon the idea that populations of the same species (or closely related species) share similar life history strategies, meta-analytic methods have been developed that allow SR parameter estimates from several populations to be combined (Myers and Mertz 1998; Myers et al. 1999; Myers et al. 2001). The analyses provide probability distributions for the SR parameters at some higher organizational level (e.g., the species) and may be used as priors for Bayesian analyses (Hilborn and Walters 1992; Carlin and Louis 1996) of population dynamics for stocks where little or no data exist about the stock under investigation. When these priors are combined with data for the population of interest, the resulting joint posterior distribution for the population-specific SR parameters include information about the population under investigation as well as information obtained from similar populations. The posterior distribution can then be used to estimate a reference *F*, using either its mode (analogous to the MLE of F_{msy} from single species data), the marginal distribution for the slope at the origin, or by finding the fishing mortality rate that maximizes the expectation of the catch over the posterior distribution for the SR parameters.

Table 1
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In summary, fisheries biologists have several options for estimating a reference *F* depending upon the available data (Table 1). In the absence of sufficient data for a production model, the researcher may choose to use an alternative reference point (e.g., $F_{x\%}$), or may use a decision theoretic approach by assuming all parameter values within some bounds are equally plausible. When the researcher has sufficient population specific data for a production model, other options are available. The researcher may calculate F_{msy} using either the maximum likelihood estimates of the SR parameters or the mode of the marginal probability distribution for slope at the origin (we will refer to this reference point as F_{marg} to distinguish it from the MLE-based estimate of F_{msy}). Alternatively, the researcher may use a decision theoretic approach such as finding the fishing mortality rate that maximizes the expectation of the yield based on the likelihood surface for the SR parameters. If the researcher does not have population specific SR data, but has priors for the SR parameters obtained from other populations, reference fishing mortality rates may be found in similar ways. The researcher may estimate a reference *F* using either the mode of the joint prior distribution for the SR parameters, the mode of the marginal probability distribution for the maximum rate that spawners produce recruits, or by finding the fishing mortality rate that maximizes the expectation of the yield. Finally, when both population specific data and data from other populations are available, the joint posterior distributions for the SR parameters may be obtained and used to estimate reference *F*'s. In the following sections, we apply these methods, and address the question of which is best for estimating a reference fishing mortality rate.

Estimating reference fishing mortality rates using population-specific data

In this section, we compare three methods of estimating reference *F*'s when only population specific data is available. We use data from two anadromous alewife, *Alosa pseudoharengus*, populations as examples: the Gaspereau River, NS, and Miramichi River, NB. Both populations are exploited commercially as they ascend their natal rivers to spawn. Descriptions of the fisheries and data collection are provided by Chaput and Atkinson (2001) and Gibson and Myers (2001). Gibson and Myers (2003b) provide details of the assessment modeling used to estimate the SR time series, maturity rates and natural mortality rates.

For estimating F_{marg} and $F_{\mathrm{maxE[Y]}}$, we will need to place bounds on the range of plausible SR parameter values. We make use of a meta-analysis of the population dynamics of eight alewife populations out using mixed effects models (Gibson and Myers 2003b). One purpose of this analysis was to derive probability distributions for the logarithm of the lifetime maximum reproductive rate (Myers et al. 1999) and the logarithm of the carrying capacity per unit area for alewife at the species level, assuming normal distributions for these parameters. The resulting random effects distribution for the log of the lifetime maximum reproductive rate has a mean of 3.06 and a standard deviation of 0.1. The random effects distribution for the log of the carrying capacity has a mean of 4.01 and standard deviation of 0.41. These estimates suggest that at low population sizes and in the absence of anthropogenic mortality, one alewife can produce about 21.3 age-3 recruits throughout its life, and that the carrying capacity for a typical alewife population is about 55 t·km^{-2} of nursery area. We will also use these distributions as informative priors when estimating reference *F*'s in a later section.

Maximum likelihood estimation of F_{msy}

F_{msy} may be estimated using surplus production models, spawner-recruit models for semelparous species, delay difference models, and age-structured production models (Quinn and Deriso 1999). Here, we estimate F_{msy} using a production model for alewife consisting of three parts: a spawner-recruit relationship, a spawning biomass per recruit model, and a yield per recruit model. Gibson and Myers (2003a) found that the Beverton-Holt SR model provided a consistently better fit to alewife spawner-recruit data than did the Ricker model. The Beverton-Holt spawner-recruit model gives the number of recruits (defined here as the number of offspring that survive to age 3) in year *t*+3, R_{t+3}, as a function of the spawning biomass in year *t*, SSB_t:

$$(1) \qquad R_{t+3} = \frac{\alpha SSB_t}{1 + (\alpha SSB_t / R_0)}.$$

Here, α is the slope at the origin and in the deterministic model is the maximum rate at which spawners can produce recruits at low population sizes in a single year (Myers et al. 1999). This term, together with the SPR model (see below), determines the maximum annual reproductive rate (the maximum rate at which spawners produce replacement spawners annually), as well as the maximum lifetime reproductive rate, defined as the maximum rate at which spawners can produce replacement spawners throughout their lives (Myers et al. 1999).

In this model, R_0 is the asymptotic recruitment level, and is the limit approached by R_t as SSB_t approaches infinity (note that the Beverton-Holt model is often written in terms of the half saturation constant, K, which is related to R_0 by: $R_0 = \alpha K$). Parameter estimates may be obtained using maximum likelihood. Assuming a lognormal error structure (Myers et al. 1995), the log-likelihood is given by:

$$(2) \qquad \ell(\alpha, R_0, \sigma) = -n \log \sigma \sqrt{2\pi} - \sum \log R_i - \frac{1}{2\sigma^2} \sum \log \left(\frac{R_i}{g(SSB_i)} \right)^2$$

where SSB_i and R_i are the observed spawner biomass and recruitment data, $g(SSB_i)$ is the Beverton-Holt spawner-recruit function, σ is the standard deviation of a normal distribution prior to exponentiation and n is the number of paired SR observations.

The second model component is the SPR model which gives the rate at which recruits produce spawners as a function of fishing mortality (Shepherd 1982; Mace and Sissenwine 1993; Mace 1994). For in-river alewife fisheries (Gibson and Myers 2003a), this is:

$$\begin{aligned}
&SPR_F = \sum_{a_{rec}}^{a_{max}} SS_a w_a e^{-F} \\
&\text{where } SS_a \text{ is given by:} \\
&SS_3 = m_3 \\
&SS_4 = SS_3 e^{-(M^{adult}+F)} + (1-m_3)e^{-M^{juv}} m_4 \\
&SS_5 = SS_4 e^{-(M^{adult}+F)} + (1-m_3)(1-m_4)e^{-2M^{juv}} m_5 \\
&SS_6 = SS_5 e^{-(M^{adult}+F)} + (1-m_3)(1-m_4)(1-m_5)e^{-3M^{juv}} m_6 \\
&. \\
&. \\
&SS_{a_{\max}} = SS_{a_{\max}-1} e^{-(M^{adult}+F)} + (1-m_3)(1-m_4)...(1-m_{a_{\max}-1})e^{-(a_{\max}-3)M^{juv}} m_{a_{\max}}
\end{aligned} \tag{3}$$

Here, a is the age of the fish, m_a is the probability that a fish that is alive at age a will mature at that age, M^{adult} and M^{juv} are as the instantaneous natural mortality rates for adult and juvenile alewife respectively and w_a is the weight at age. These values are fixed constants in this analysis, although the decision theoretic methods presented herein could be extended to include uncertainty in these parameters.

In-river alewife fishing seasons are typically relatively short (about a month) with the majority of the catch being taken during a couple weeks. As a result, the effects of natural and fishing mortality occurring concurrently can be ignored when estimating the yield per recruit. The yield per recruit for a given F (YPR_F) is thus found analogously to the spawning biomass per recruit:

$$YPR_F = \sum_{a_{rec}}^{a_{max}} SS_a w_a (1-e^{-F}) \ . \tag{4}$$

For a given value of F, the spawning biomass produced by a given number of recruits in year t (throughout their lives) is $SSB = SPR_F \cdot R_t$. Equilibrium spawning biomass and recruitment levels may be found by solving this equation for R_t, and substituting the result in the spawner-recruit model (Quinn and Deriso 1999). For a given α and R_0 pair, the equilibrium yield ,Y^*, can be calculated for each value in a set of F's, and F_{msy} can be found using a search over the set to find the fishing mortality where Y^* is maximized. If the maximum likelihood estimates of α and R_0 are used, the maximum likelihood estimate of F_{msy} is obtained. This is the most common method of estimating F_{msy}, but does not include uncertainty in the SR parameters in the selection of a reference F.

The data for both alewife populations show considerable variability about the fitted SR model (Figure 1). For the Gaspereau River population, all observed SSB's are low relative to the estimated equilibrium unfished spawner biomass, and all but three are below SSB_{msy}. The SR parameter estimates ($\alpha = 96.1,\ R_0 = 1.6\,\text{million}, \sigma = 0.42$) obtained from these data appear biologically realistic, although given the limited range of the observed spawner biomasses, at least the estimate of the asymptotic recruitment level is questionable. The SSB's for the Miramichi alewife population have a greater range than for the Gaspereau River, but the data exhibit greater variability about the fitted SR relationship. The SR parameter estimates for this population ($\alpha > 1\,\text{billion},\ R_0 = 7.4\,\text{million}, \sigma = 0.94$) are biologically unrealistic: the estimate of α exceeds the fecundity of the fish, and the parameter estimates suggest that a spawner biomass of ten grams can produce half the recruitment of a spawner biomass of a million kilograms. Estimates of F_{crash} (the fishing mortality rate that drives the population to extinction) and F_{msy} from the Miramichi data exceed 5.0 suggesting that the population cannot be overfished and are simply not believable.

Figure 1
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Evaluating uncertainty in F_{msy}

These examples illustrate some of the problems that may be encountered when deriving reference fishing mortality rates from noisy SR data. In the case of the Miramichi River population, the SR parameter estimates and resulting reference points are clearly unrealistic. Nonetheless, management advice often has to be provided when only data of this type is available. Plausible estimates are obtained for the Gaspereau River population, although they may be questionable given the limited range of the data.

The plausibility of an individual parameter estimate can be assessed by examining its log profile likelihood (Davison and Hinkley 1997). The log profile likelihood for α, $\ell_{\mathrm{p}}(\alpha)$, is:

$$(5) \qquad \ell_{\mathrm{p}}(\alpha) = \max_{R_0 \sigma} \ell(\alpha, R_0, \sigma).$$

The maximum likelihood estimate for α occurs where $\ell_{\mathrm{p}}(\alpha)$ achieves is maximized. The plausibility of other possible values of α is evaluated by comparing their log profile likelihoods with the maximized log profile likelihood. A likelihood ratio based 95% confidence interval for α is:

$$(6) \qquad \{\alpha : 2\left[\ell_p(\alpha^{\mathrm{MLE}}) - \ell_p(\alpha)\right] \leq \chi_1^2(0.95)\}.$$

The profile likelihood and the associated 95% confidence interval for R_0 were found similarly, and for F_{msy} by mapping from the profile likelihood for α to F_{msy} using the production model.

The log profile likelihood for α for the Miramichi population is ramped: the lower bound of the 95% confidence interval for α is determined, but the maximum likelihood estimate and its upper bound are essentially infinite (Figure 2). For the Gaspereau River population, the MLE of α and the lower bound of its 95% confidence interval may be estimated, but $\ell_{\mathrm{p}}(\alpha)$ decreases only very slightly above the MLE. The asymptotic recruitment level is better determined by the data although the upper and lower 95% confidence limits differ by a factor of about 5 times. The pattern for F_{msy} is similar to that of α; only the lower bound is determined by the data. Clearly, for data sets similar to these, the MLE of the SR parameters and the associated estimates of F_{msy} are not good reference points for fishery management.

Figure 2
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The log likelihood surfaces for α and R_0 (Figure 2) provide a basis for assessing the plausibility of pairs of parameter values. The surfaces for both the Gaspereau River and Miramichi populations show an "L"-shaped ridge, along which the likelihood changes only slightly. This implies that the likelihood of observing the data is similar, given either low values of α and high values of R_0, or high values of α and low values of R_0. One cannot choose between these scenarios on the basis of the data, and these surfaces again show the considerable uncertainty associated with the MLE of F_{msy}.

Estimating reference *F*'s that include SR parameter uncertainty

For both the Miramichi and Gaspereau River alewife populations, there are plausible values of α (not significantly different from the MLE of α at a 95% confidence level) for which there exists the possibility that the asymptotic recruitment level is substantially higher than its MLE. The data therefore do not preclude the possibility of larger recruitments, suggesting that the subsequent yield could potentially increase if the fishing mortality rate was set below the MLE for F_{msy}. The data also suggest that larger recruitments are less plausible at the MLE for α than at lower values for this parameter. An appropriate reference fishing mortality rate should not preclude the possibility of achieving larger catches, particularly if the reference rate is not significantly different from the MLE of F_{msy}. In this section, we demonstrate the two alternative methods of deriving reference fishing mortality rates that include SR parameter uncertainty: the use of the mode of the marginal probability density for α to determine F_{marg} and finding the fishing mortality rate that maximizes the expectation of the catch, $F_{\mathrm{maxE[Y]}}$.

We begin by selecting a parameter space, Ω, for the SR model with two dimensions: α and R_0. Any point in this parameter space may be viewed as a separate hypothesis about the SR relationship for each population. We used $\alpha = \dfrac{1}{SPR_{F=0}}$ as the lower limit for α for each population. Below this limit, the population would go extinct because reproduction would not be sufficient to offset natural mortality. We set the upper bound for α at 250. We used the 1st and 99th percentiles of the random effects distribution of R_0 for the bounds on R_0. The joint Bayesian posterior distribution is given by:

$$(7) \qquad p(\alpha, R_0) = \left\{ \begin{array}{cr} \dfrac{L(\mathbf{R}\,|\,\mathbf{S},\alpha,R_0)\cdot p(\alpha)\cdot p(R_0)}{\iint\limits_{\Omega} L(\mathbf{R}\,|\,\mathbf{S},\alpha,R_0)\cdot p(\alpha)\cdot p(R_0)d\alpha dR_0}, & \alpha, R_0 \in \Omega \\ 0 & \text{otherwise} \end{array} \right\}$$

where $L(\mathbf{R}\,|\,\mathbf{S},\alpha,R_0)$ is the probability of observing the data for a given pair of parameter values, and $p(\alpha)$ and $p(R_0)$ are the prior probabilities that are the probabilities for alternative values for the parameters, before considering data for the population under consideration. In this section, we assume uniform priors over the intervals above; more informative priors are considered in a later section. The marginal probability distribution for α is calculated from the posterior distribution as:

$$(8) \qquad p(\alpha \mid p(\alpha, R_0)) = \int p(\alpha, R_0) dR_0$$

The mode of the resulting probability density provides an alternative estimate of α that is used to calculate F_{marg}.

For a given F, the expectation of the equilibrium yield is given by:

$$(9) \qquad E\left[Y^*(F)\right] = \int\int Y^*(F, \alpha, R_0) p(\alpha, R_0) dR_0 d\alpha$$

where $Y^*(F, \alpha, R_0)$ is the equilibrium yield as a function of the fishing mortality rate, α and R_0, and $p(\alpha, R_0)$ is the posterior density evaluated at α and R_0. The fishing mortality rate that maximizes the expectation of the yield is then:

$$(10) \qquad F_{\max\ \mathrm{E[Y]}} = \underset{F}{\mathrm{argmax}}\ \ \mathrm{E}\left[Y^*(F)\right].$$

Estimates of $F_{\mathrm{maxE[Y]}}$ could be obtained without SR data simply by assuming that all values for the SR parameters within some range were equally probable. Plausible estimates were obtained using this method, although the estimates are sensitive to the assumed range. When the population specific data are included, the estimates of F_{marg} and $F_{\mathrm{maxE[Y]}}$ are less

Table 2
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than the MLE of F_{msy} for both the Gaspereau and Miramichi River alewife populations (Table 2). While the MLE of F_{msy} for the Miramichi River population was essentially infinite, plausible estimates of F_{marg} and $F_{\mathrm{maxE[Y]}}$ could be obtained. For the Gaspereau River population, the exploitation rate corresponding to F_{marg} was 0.7 lower than that corresponding to the MLE of F_{msy},. The exploitation rate corresponding to $F_{\mathrm{maxE[Y]}}$ was between these values.

Comparison of F_{msy}, F_{marg} and $F_{\mathrm{maxE[Y]}}$

Both F_{marg} and $F_{\mathrm{maxE[Y]}}$ provided estimates of reference fishing mortality rates that were lower than F_{msy} for Gaspereau River alewife. These reference points could also be calculated for the Miramichi River population, for which the estimate of F_{msy} was essentially infinite. Additionally, these reference points are intuitively appealing, because uncertainty in the SR relationship is explicitly included in their estimation. In this section, we compare the performance of these three reference points using a Monte Carlo simulation model.

The simulation model is based on the production model used to estimate F_{msy}. We ran simulations for 25 combinations of α (values: 10, 25, 50, 100, 250) and σ (0.1, 0.3, 0.5, 0.7, 0.9). A constant K was used for all simulations. For each combination, we simulated 500 SR data sets, randomly choosing 20 spawner biomasses between zero and the unfished equilibrium spawner biomass for each simulation. Recruitments were assigned to each spawner biomass by randomly selecting a value from a lognormal distribution with its mean determined by the SR function:

$$(11) \qquad R_i = \frac{\alpha SSB_i}{1+\frac{SSB_i}{K}} \exp\left(\varepsilon_i\sigma - \frac{\sigma^2}{2}\right), \quad where\ \varepsilon_i \sim N(0,1).$$

The same random numbers were used for each set of 500 simulations to ensure that any differences detected were not an artefact of the random number generation. The reference points F_{msy}, F_{marg}, and $F_{\mathrm{MaxE[Y]}}$ were calculated for each dataset as described in the previous sections.

Figure 3 near here

At low levels of recruitment variability, the three references points performed similarly (Figure 3). However, both F_{marg} and $F_{\mathrm{maxE[Y]}}$ consistently underestimated the true F_{msy} at higher levels of σ, whereas the MLE of F_{msy} was the least biased estimator of the true F_{msy}. However, the maximum likelihood estimate was the most variable estimator, at times substantially overestimating or underestimating the true F_{msy}. At higher levels of α and σ, $F_{\mathrm{maxE[Y]}}$ had the least variability.

Figure 4 near here

Figure 5 near here

Do the benefits of least biasness outweigh the cost of high variability when choosing a method of estimating a reference *F*? We addressed this question by comparing the equilibrium yield, spawner biomass, yield per recruit and spawning biomass per recruit that would result if the estimated reference *F*'s were applied to a population with the dynamics used to simulate the data. Using the case of $\alpha = 50$ and $\sigma = 0.9$ as an example, about 25% of the populations would be highly overexploited if fished at the estimated MLE of F_{msy}, and 13.4% of the populations would be fished to extinction at this rate (Figure 4). None of the populations would be highly overexploited when fished at F_{marg} or $F_{\mathrm{maxE[Y]}}$ (Figure 4). Differences in mean equilibrium yield, spawner biomass, yield per recruit and spawning biomass per recruit resulting from the three reference *F*'s were small at low levels of recruitment variability, but increased as variability increased (Figure 5). On average, $F_{\mathrm{maxE[Y]}}$ produces higher yields than either F_{msy} or F_{marg} while maintaining spawner biomasses that are on average higher than F_{msy}, but slightly lower than F_{marg} (Figure 5). In the example of α=50 and σ=0.9, the mean equilibrium catch obtained using $F_{\mathrm{maxE[Y]}}$ as a reference F exceeded the mean equilibrium catch obtained using F_{msy} as a reference F by a factor of 1.19, while maintaining spawner biomasses that were higher by a factor of 1.34. $F_{\mathrm{maxE[Y]}}$ typically produced YPR values between those of F_{msy} and F_{marg}, although these differences were small (Figure 5). F_{marg}, the most conservative reference point maintained the highest SPR levels.

Including information from other populations

The decision theoretic approach of maximizing the expectation of the yield is easily extended to include information from other populations. We used the random effects distribution for the log of the maximum lifetime reproductive rate and for the log of the adult carrying capacity obtained by Gibson and Myers (2003b) to derive empirical priors for the SR for α and R_0. The maximum likelihood estimates of the random effects distributions, known as MLE priors (Efron 1996), are used in the empirical Bayes analysis that follows. The priors are obtained by standardizing the random effects distributions by amount of nursery area available for each population, and converting from carrying capacity for adult fish and the maximum lifetime reproductive rate to R_0 and α by dividing by $SPR_{F=0}$. These priors contain the information about the distribution of these parameters at the species level obtained by analyzing data from other alewife populations.

Figure 6 near here

The resulting empirical prior probability densities for α and R_0 for alewife are shown together with the likelihood surface for these parameters for Gaspereau River alewife in Figure 6, providing a basis for assessing the plausibility of the estimates of α and R_0 for the Gaspereau River alewife population. The maximum likelihood estimate of α is high relative to the mode of the prior for α at the species level, whereas the prior for R_0 suggests that we may be underestimating R_0 using only the population specific data. The population-specific data do not preclude the possibility of very high asymptotic recruitment levels at lower values of α, although the prior for R_0 indicates that these high asymptotic recruitment levels are not very plausible given the species level information. A different pattern is evident for the Miramichi River alewife population (Figure 6). The likelihood surface suggests that R_0 is reasonably estimated from the population specific data even though the data are largely uninformative about α. However, comparison with the priors suggests that the estimate of R_0 obtained for this population is low relative to that of other alewife populations.

During the estimation of $F_{\mathrm{maxE[Y]}}$ in the preceding section, uniform bounded priors were assumed for $p(\alpha)$ and $p(R_0)$. The priors distributions for α and R_0 obtained from the meta-analysis are more informative alternatives for $p(\alpha)$ and $p(R_0)$, and enter directly into the estimation of $F_{\mathrm{maxE[Y]}}$ through the calculation of the Bayesian joint posterior distribution, $p(\alpha, R_0)$, shown in equation 13. When the informative priors are used, the estimates of the exploitation rate corresponding to $F_{\mathrm{maxE[Y]}}$ for Gaspereau River alewife are reduced from 0.61 (uniform bounded prior) to 0.56 (Table 2). For the Miramichi River population, the estimate is reduced from 0.68 to 0.53. For both populations, the prior for α has the greatest influence on the estimates of the reference F's. As a result, the estimates obtained using only the data from the other populations and using the combined data are the same (Table 2) because the population-specific data are relatively uninformative about the true value of α in comparison with this prior (Figure 6).

Discussion

Despite being embedded in the management objectives of many organizations and countries (Quinn and Deriso 1999; Mace 2001), the concept of MSY has been the target of much criticism (e.g., Larkin 1977). These criticisms typically fall into three categories:

problems with its implementation, its appropriateness as a management goal, and problems with its estimation (Punt and Smith 2001). Implementation problems are not specific to MSY, but apply to any management objective. In recent years, the role of MSY as a management objective has undergone a shift as a result of the development of precautionary and ecosystem-based approaches to fisheries management (Mace 2001). While the difficulty with the estimation of F_{msy} remains a valid criticism of MSY, in this paper we have demonstrated that better reference fishing rates can be obtained by using the decision theoretic approach of maximizing of the expected yield and by including data from other populations when estimating a reference F.

When choosing any model-based reference point, an underlying mathematical model that reflects the fish population dynamics is also selected. Caddy and Mahon (1995) suggest that when selecting a reference point, rather than simply choosing the one with the best theoretical underpinnings, a more appropriate criterion may be picking the reference point that provides conservative advice under conditions of uncertainty. In our examples, although maximum likelihood was the least biased of the methods examined here, it provided the highest estimates for a reference F and lower average yields than the method of maximizing the expected yield, particularly when the SR data are noisy. The method of maximizing the expected yield is therefore more precautionary than the maximum likelihood method from both a conservation perspective (lower fishing mortality rates and higher spawner biomasses) and from that of maximizing yield.

In our simulations, the fishing mortality rate that maximized the expectation of the yield could be reasonably estimated from all datasets and showed much lower variability than the maximum likelihood estimate of F_{msy}. In the case of the Miramichi River alewife, the

MLE of F_{msy} was essentially infinite, whereas the exploitation rate that maximized the expected yield was 0.68. This estimate is slightly higher than the average exploitation rate at MSY for alewife (0.65) reported by Crecco and Gibson (1990), and is within the range of values reported by Gibson and Myers (2003b). However, using a life history based simulation model, the latter authors found that an exploitation rate of about 0.40 for in river alewife fisheries produced more than 90% of MSY, and suggested this to be a reasonable limit given that no allowances were made for factors such as implementation uncertainty. The inclusion of information from other populations through the use of informative priors lowered the estimated reference F's to 0.53 for the Miramichi population, providing a more conservative but reasonable reference F given the above results. Additionally, we did not obtain infinite estimates of the reference F's obtained from the mode of the marginal probability density or by maximization of the expected yield in any of the 12 500 simulated datasets in this study, although the estimates of infinite slopes at the origin (and the MLE of F_{msy}) were obtained for many of the simulated datasets. These results illustrate the problems with estimating F_{msy} using maximum likelihood, indicate that reasonable reference F's may be obtained by maximizing the expected yield even when the SR data exhibits considerable variability and shows that inclusion of information from other populations can also improve the resulting estimates.

While maximization of the yield performed well in our simulations, caution is warranted when using data with a limited spawner biomass range. For the Miramichi River population, the exploitation rate that maximized the expectation of the yield from the population-specific data was higher than when information from other populations was included. As shown in Figure 6, R_0 appears reasonably estimated for this population, but is low in comparison with other populations. While it is possible that Miramichi alewife have a higher maximum reproductive rate and lower carrying capacity than other alewife populations, a more precautionary explanation is that this result reflects limitations of the data not overcome by maximizing the expected yield using only the population specific-data. When SR data have a limited range of spawner biomasses, R_0 may appear reasonably well estimated when in fact the estimate only reflects the average recruitment in the data series. This is the case with the Miramichi alewife data as evidenced by the infinite estimate of the maximum rate that spawners produce recruits. In these instances, the resulting reference F obtained by maximizing the expected yield may still be high relative to the true F_{msy}. Comparison with parameter estimates from similar populations (e.g. Figure 6) provides a method to detect this problem. Alternatively, SR data from several populations can be standardized so that it can be plotted on the same scale. When this is done, populations with data that are dissimilar to other populations are immediately evident (Myers et al. 2001; Gibson and Myers 2003a). This method can also be used to detect populations for data is insufficient to estimate R_0.

At least in our examples, the method of maximizing the expectation of the yield clearly outperformed the maximum likelihood method of estimating F_{msy}. This finding leads to the suggestion that model fitting criteria based on management objectives may outperform those based solely on statistical criteria such as least biasness. However, in our examples, reference F's obtained from the mode of the marginal probability for the SR slope at the origin (F_{marg}) also produced higher average yields and spawner biomasses than reference F's obtained by maximum likelihood even though the F_{marg} showed the greatest bias. Also using simulations, Neilson and Lewy (2002) found that a Bayes estimate of spawning biomass in an age-structured assessment model outperformed the maximum likelihood estimate. In their example, the Bayes estimate showed less bias, but was based on the posterior mean rather than the mode. Both these analyses demonstrate the advantages of obtaining parameter estimates from the marginal probability density as opposed to maximum likelihood.

One of the most striking outcomes of our analyses is the observation that when F_{msy} was estimated from noisy SR data using maximum likelihood, a portion of the populations could be fished to extinction if the reference F was implemented. In 13.4% of the $\alpha = 50$ and $\sigma = 0.9$ simulations, the estimate of F_{msy} exceeded the fishing mortality rate that would drive the population to extinction, and would have serious consequences for the population if used as a management target. In instances where the estimate of F_{msy} is essentially infinite, the estimate is obviously wrong and would not be used as a basis for management advice. The more serious problem occurs at low α's when it may not be obvious when the MLE of F_{msy} exceeds the productive capacity of the population. Based on our simulations, this problem is alleviated by changing the optimization criteria for estimating the reference F: none of the simulated populations would be fished at a rate that cause extinction if fished at the rate obtained by maximizing the expectation of the yield.

The use of meta-analysis is becoming more common in fisheries science (e.g., Harley and Myers 2001; Chen and Holtby 2002; Dorn 2002). For many species of fish, probability distributions for the maximum reproductive rate have been derived at the species and family levels (Myers et al. 1999), and for categories based on life history strategies (Myers et al 2002). In this paper, we have shown how these distributions can be used to evaluate reference points based on stock-specific analyses, to place bounds on the range of plausible values for the SR parameters (see also Brodziak 2002), and be incorporated directly into reference point estimation. In our analyses, the priors for α and R_0 were much more informative than the data for either population, and therefore dominated the reference point estimation procedure. Gibson and Myers (2003b) do not preclude the possibility that the variance for α was underestimated in their analysis. Increasing the variance on the prior for α without changing its mean decreases the resulting reference F obtained by maximizing the expected yield.

The idea that reference points are more conservative when uncertainty is included in their estimation is not new. Ludwig and Walters (1982) found that in an active adaptive policy, inclusion of parameter uncertainty lead to higher target spawning escapements, although lower escapements could also lead to higher long term yields if they resulted in a reduction in parameter uncertainty. Walters and Pearse (1996) concluded that uncertainty in stock size estimates would significantly lower allowable catches as low-risk management policies are adopted. Decision theory provides a method for incorporating uncertainty into the decision framework through the use of a loss function. Finding the fishing mortality rate that maximizes the expected yield provides a decision theoretic reference point with a risk neutral loss function because the magnitude of the equilibrium catch is used in its calculation. Risk adverse approaches may also be implemented without substantial modifications to the method by weighting or transforming the yield prior to maximizing the expected yield.

Both the Miramichi and Gaspereau River alewife populations have yield per recruit relationships that are ramped (Gibson and Myers 2003b). The method of maximizing the expected yield given uncertainty in the SR parameters is most appropriate for fisheries similar to the fisheries on these rivers (a non-selective fishery on fish that are relatively full grown prior to recruiting to the fishery). For populations with a well determined F_{max} (typically a fishery that catches fish over a wider size range), assumptions about the selectivity pattern, growth and survival will have greater influence on F_{msy} than in our examples. If the uncertainly associated with these parameters is quantified, it can also be included in when estimating a reference F using the method of maximizing the expected yield.

In summary, the analyses presented herein indicate that using decision theoretic methods that evaluate the quantities of interest, i.e. fishing mortality and yield, outperform more indirect methods, i.e. using maximum likelihood estimates of SR parameters to derive the fishing mortality rate that produces maximum sustainable yield. The decision theoretic reference fishing mortality rate was more conservative, produced higher yields and spawner biomasses a while reducing the probability of under- or over-exploiting the population in comparison with the maximum likelihood estimate of F_{msy}. Additionally, when data from other populations is available, they can be used either to assess the plausibility of parameter estimates, or incorporated directly into the reference point estimation process. In these ways, the use of fishery reference points as guide to fishery management can be improved.

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Table 1. Summary of methods for estimating reference fishing mortality rates. Methods are presented in the context of the Beverton-Holt SR model, parameterized in terms the slope of the model at the origin of the SR model (α) and the asymptotic recruitment level (R_0). The maximum likelihood methods use the mode of the SR likelihood or probability surface as the estimate of α that is used to estimate F_{msy}. The marginal probability density for α is found by integrating over R_0 and the optimal F is estimated using the mode of the resulting distribution. The decision theoretic method finds the value of F that maximizes the expectation of the catch over α and R_0.

Data requirements	Maximum likelihood and alternatives	Marginal probability density for α	Decision theoretic methods
Insufficient data for a production model	Alternatives: F_{med}, $F_{\mathrm{x\%}}$, $F_{0.1}$		F_{mmy} $F_{\mathrm{maxE[Y]}}$ (uniform bounded prior)
Population specific data only	F_{msy} from the M.L.E. of α and R_0	Integration of the likelihood over R_0 (F_{marg})	$F_{\mathrm{maxE[Y]}}$ (likelihood only)
Data from other populations only	F_{msy} from the mode of the prior for α and R_0	Integration of the prior for α and R_0 over R_0 (F_{marg})	$F_{\mathrm{maxE[Y]}}$ (priors only)
Combined data	F_{msy} from the mode of posterior for α and R_0)	Integration of the posterior for α and R_0 over R_0 (F_{marg})	$F_{\mathrm{maxE[Y]}}$ (priors and likelihood)

Table 2. Reference exploitation rates for two alewife populations in the Maritime Provinces, Canada, estimated without spawner-recruit data, using population-specific spawner-recruit data and using spawner-recruit data from other populations. Estimates are obtained using either the mode of joint likelihood or probability distributions (F_{msy}), the marginal likelihood or probability density for α (F_{marg}) or by finding the fishing mortality rate that maximizes the expectation of the catch ($F_{\mathrm{maxE[Y]}}$).

Reference point	Exploitation Rate	
	Gaspereau River	Miramichi River
No data:		
$F_{\mathrm{maxE[Y]}}$ (uniform bounded probability surface)	0.61	0.63
Population-specific data only:		
F_{msy} (maximum likelihood estimate)	0.63	>0.99
F_{marg} (mode of the marginal likelihood for α)	0.56	0.77
$F_{\mathrm{maxE[Y]}}$ (joint likelihood for α and R_0)	0.61	0.68
Data from other populations only:		
F_{msy} (mode of joint prior distribution for α and R_0)	0.56	0.53
F_{marg} (mode of the marginal probability density for α based on the joint prior distribution)	0.56	0.53
$F_{\mathrm{maxE[Y]}}$ (joint prior distribution for α and R_0)	0.56	0.53
Combined data:		
F_{msy} (mode of joint posterior distribution for α and R_0)	0.56	0.53
F_{marg} (mode of the marginal probability density for α based on the joint posterior distribution)	0.56	0.53
$F_{\mathrm{maxE[Y]}}$ (joint posterior distribution for α and R_0)	0.56	0.53

Figure Captions:

Figure1. Beverton-Holt spawner-recruit (SR) models (solid line) and production model reference points for the Gaspereau River (a) and Miramichi River (b) alewife (*Alosa pseudoharengus*) populations. The SR models are the maximum likelihood fits assuming lognormal errors. The dotted line is the replacement line in the absence of fishing mortality. The slope of the SR model at the origin was essentially infinite for the Miramichi population, and reference points could not be estimated for that population.

Figure 2. Contour plots (a) showing the joint log likelihood surface for the slope at the origin of the spawner-recruit (SR) model and the asymptotic recruitment level for the Gaspereau River (left column) and Miramichi River (right column) alewife populations. The black square indicates the point at which the log likelihood is maximized (not available for the Miramichi population). The contour interval is -1 moving away from this point. The grey-shaded region shows the likelihood based 95% joint confidence region for the parameters. Profile log likelihoods (solids lines) are shown for the slope at the origin (b), the asymptotic recruitment level (c) and the fishing mortality rate at maximum sustainable yield (d), the later obtained from the profile likelihood for the slope at the origin of spawner-recruit model. The log likelihoods are standardized to a maximum of 0 by subtracting the maximum log likelihood from each estimate. The intersections between the dotted lines and the profile likelihoods show likelihood ratio based 95% confidence intervals for each parameter. Upper and lower bounds cannot be determined for the slope at the origin or F_{msy} for either population.

Figure 3. A summary of the simulation results comparing reference fishing mortality rates estimated using maximum likelihood estimation (M.L.E.), the mode of the marginal

probability density (M.P.D.) and a decision theoretic model (D.T.). The resulting reference points are referred to in the text as F_{msy}, F_{marg}, and $F_{\mathrm{maxE[Y]}}$. The box plots show the distributions of the estimated reference fishing mortality rates for 500 simulated spawner-recruit datasets for each combination of α (alpha) and σ (sigma). The median value is indicated with a point and the grey shaded region shows the inter-quartile range. The whiskers are drawn to the nearest value within 1.5 times the inter-quartile range. The dotted line gives the true F_{msy} for the simulated dynamics.

Figure 4. A summary of the simulation results for values of alpha = 50 and sigma = 0.9. The solid line gives the known equilibrium yield, scaled to a maximum of one, as a function of the exploitation rate. The box plots show the distribution of the reference fishing mortality rates estimated from 500 simulated spawner-recruit datasets using the three methods. The maximum likelihood method produces the maximum likelihood estimate of F_{msy}, the marginal probability method uses the mode of the marginal probability density for the maximum reproductive rate to obtain a reference F (F_{marg}) and a reference F is found using the decision theoretic method by maximizing the expected yield ($F_{\mathrm{maxE[Y]}}$). For each method, the solid line is the median value and the grey shaded region shows the inter-quartile range. The whiskers are drawn to the nearest value within 1.5 times the inter-quartile range. Points beyond these limits are plotted as points.

Figure 5. The relationship between the mean equilibrium catch (row a), mean spawner abundance (row b), mean spawning biomass per recruit (row c), and mean yield per recruit (row d) for three methods of estimating reference fishing mortality rates and the variability in the spawner-recruit data (sigma), based on 500 simulated SR datasets for each combination of alpha and sigma. Mean equilibrium values were calculated by applying the estimated

reference fishing mortality rates for each dataset to the known dynamics used to simulate the data. The dotted line shows equilibrium values that result when the maximum likelihood estimate of the maximum reproductive rate (alpha) is used to estimate F_{msy}, the dashed line shows the values that result when the mode of the marginal probability is used to estimate a reference F (F_{marg}) and the solid line shows equilibrium values obtained by fishing at the decision theoretic reference point $F_{\mathrm{maxE[Y]}}$.

Figure 6. A comparison of the joint log-likelihood surface (a,d) for the slope at the origin and the asymptotic recruitment level with the random effects distributions for the slope at the origin (b,e) and the asymptotic recruitment level (c,f) for 2 alewife (*Alosa pseudoharengus*) populations. The random effects distributions are derived from a meta-analysis of eight alewife populations and depict the distribution of the spawner-recruit parameters for alewife at the species level, and are scaled by the amount of nursery area available for these populations. The black square in the log-likelihood surface shows the point where the log-likelihood is maximized. The contour interval is -1 moving away from this point. The grey-shaded region shows the likelihood ratio based 95% confidence region for the parameters.

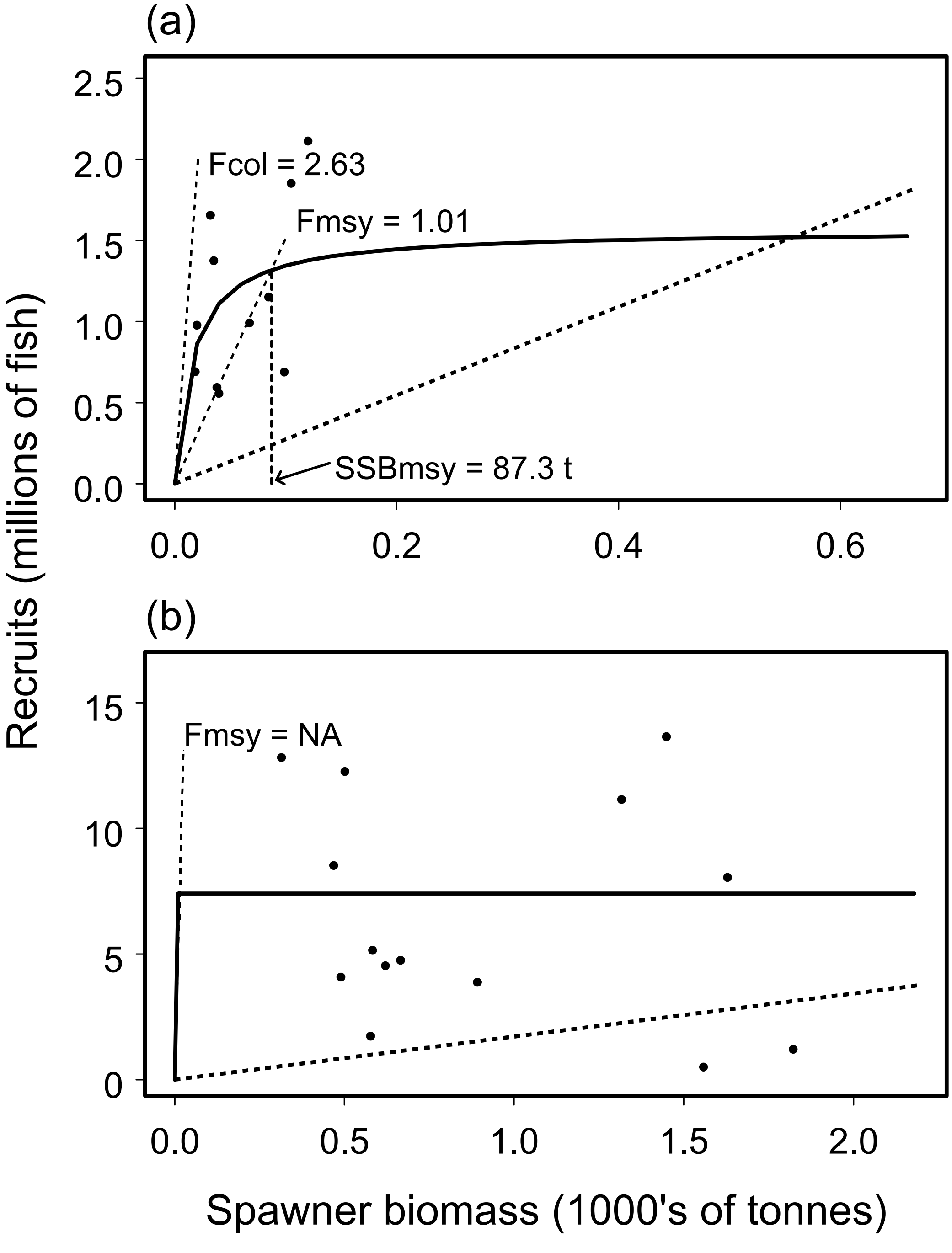
(a)
2.5
2.0
1.5
1.0
0.5
0.0
Fcol = 2.63
Fmsy = 1.01
SSBmsy = 87.3 t
0.0
0.2
0.4
0.6
(b)
15
10
5
0
Fmsy = NA
0.0
0.5
1.0
1.5
2.0
Recruits (millions of fish)
Spawner biomass (1000's of tonnes)

Figure 1.

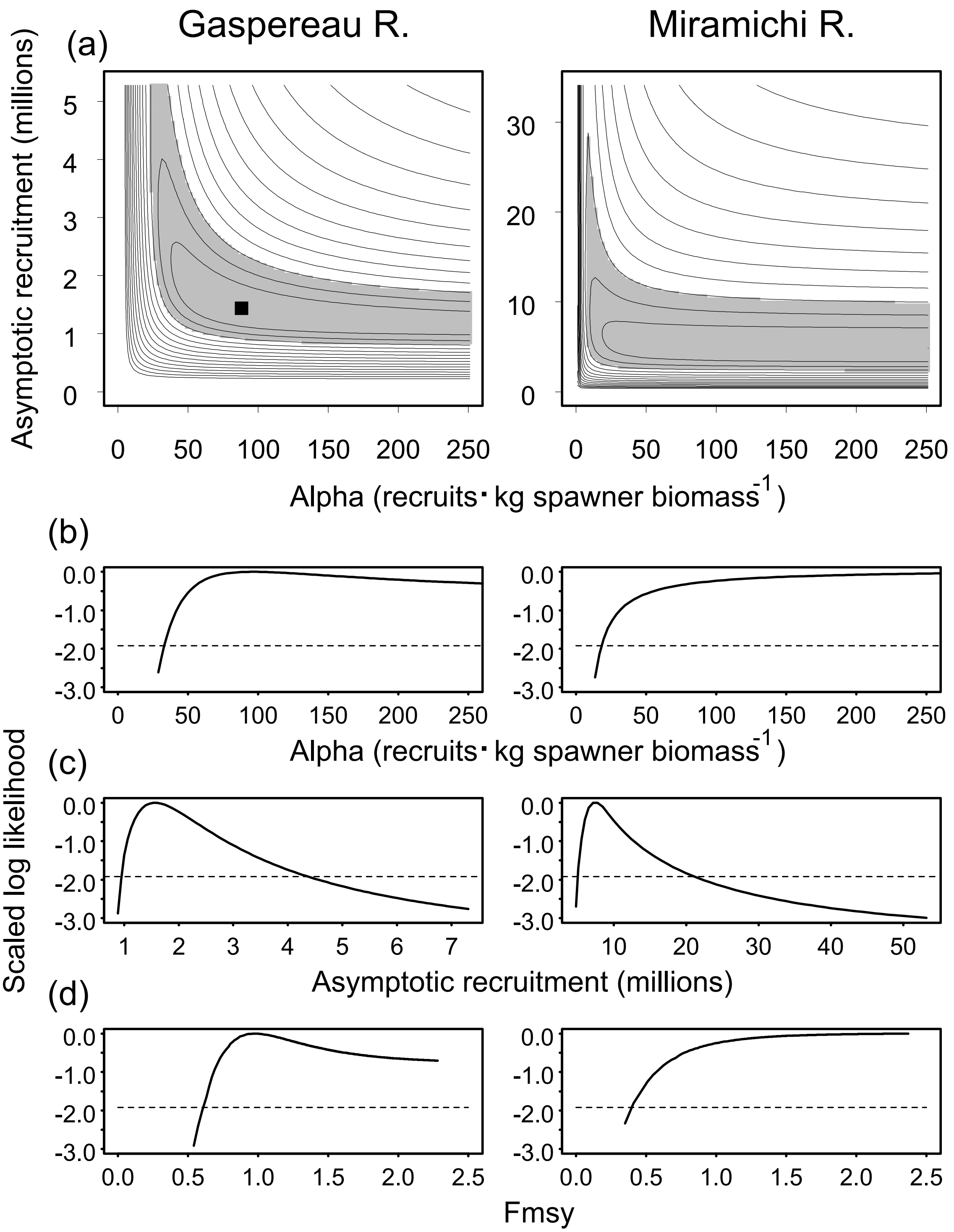
Gaspereau R.
Miramichi R.
(a)
Asymptotic recruitment (millions)
0
1
2
3
4
5
0
10
20
30
0
50
100
150
200
250
Alpha (recruits · kg spawner biomass^{-1})
(b)
0.0
-1.0
-2.0
-3.0
Alpha (recruits · kg spawner biomass^{-1})
(c)
Scaled log likelihood
1
2
3
4
5
6
7
10
20
30
40
50
Asymptotic recruitment (millions)
(d)
0.0
0.5
1.0
1.5
2.0
2.5
Fmsy

Figure 2.

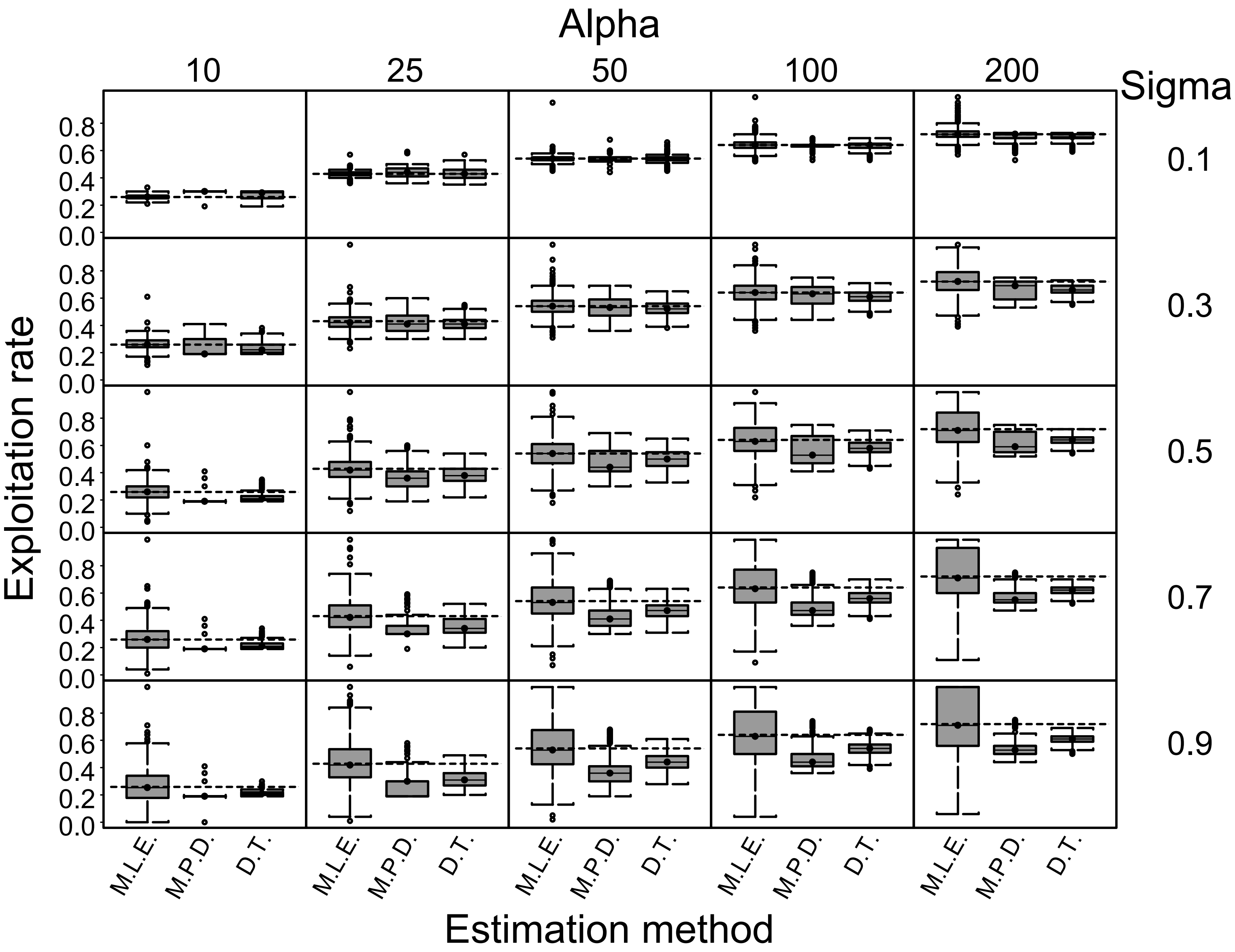
Alpha
10
25
50
100
200
Sigma
0.1
0.3
0.5
0.7
0.9
Exploitation rate
0.0
0.2
0.4
0.6
0.8
M.L.E.
M.P.D.
D.T.
Estimation method

Figure 3.

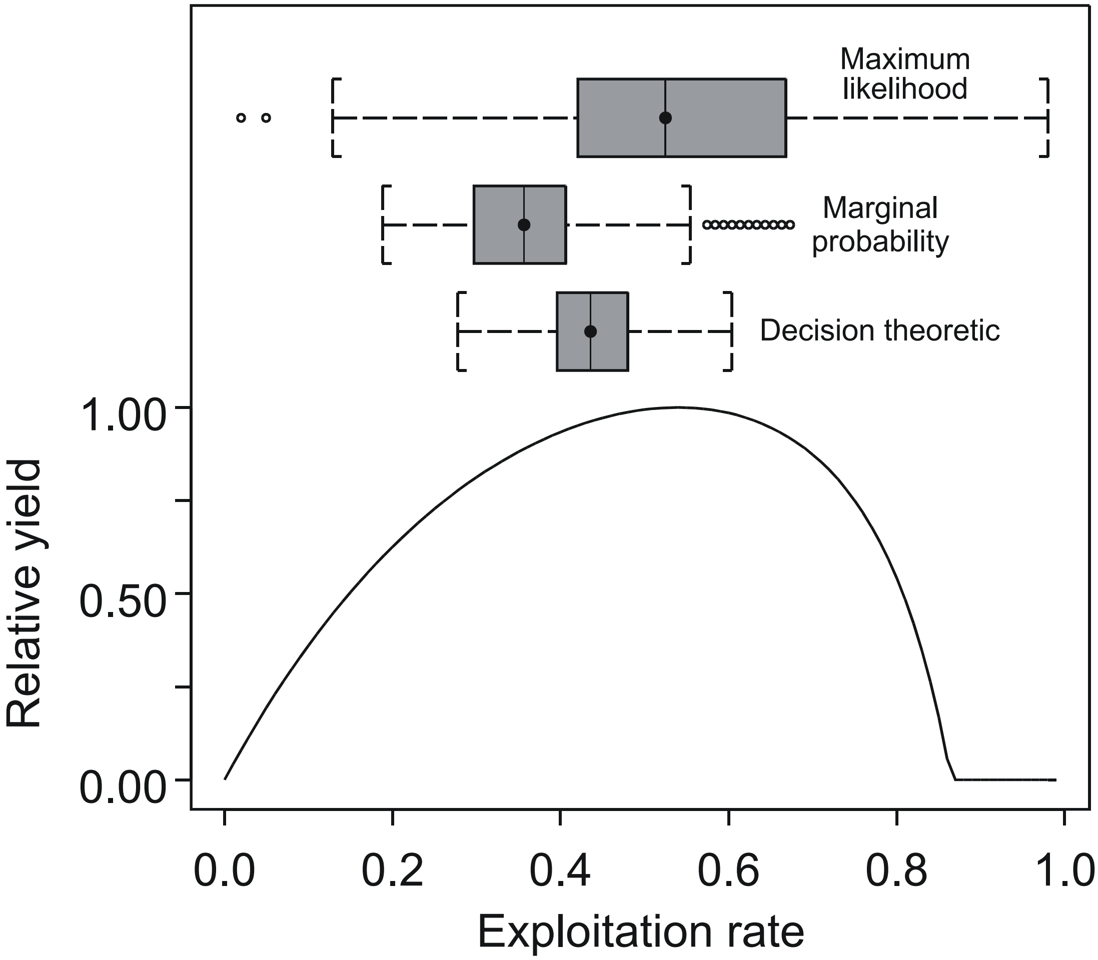
Maximum likelihood
Marginal probability
Decision theoretic
1.00
0.50
0.00
Relative yield
0.0
0.2
0.4
0.6
0.8
1.0
Exploitation rate

Figure 4.

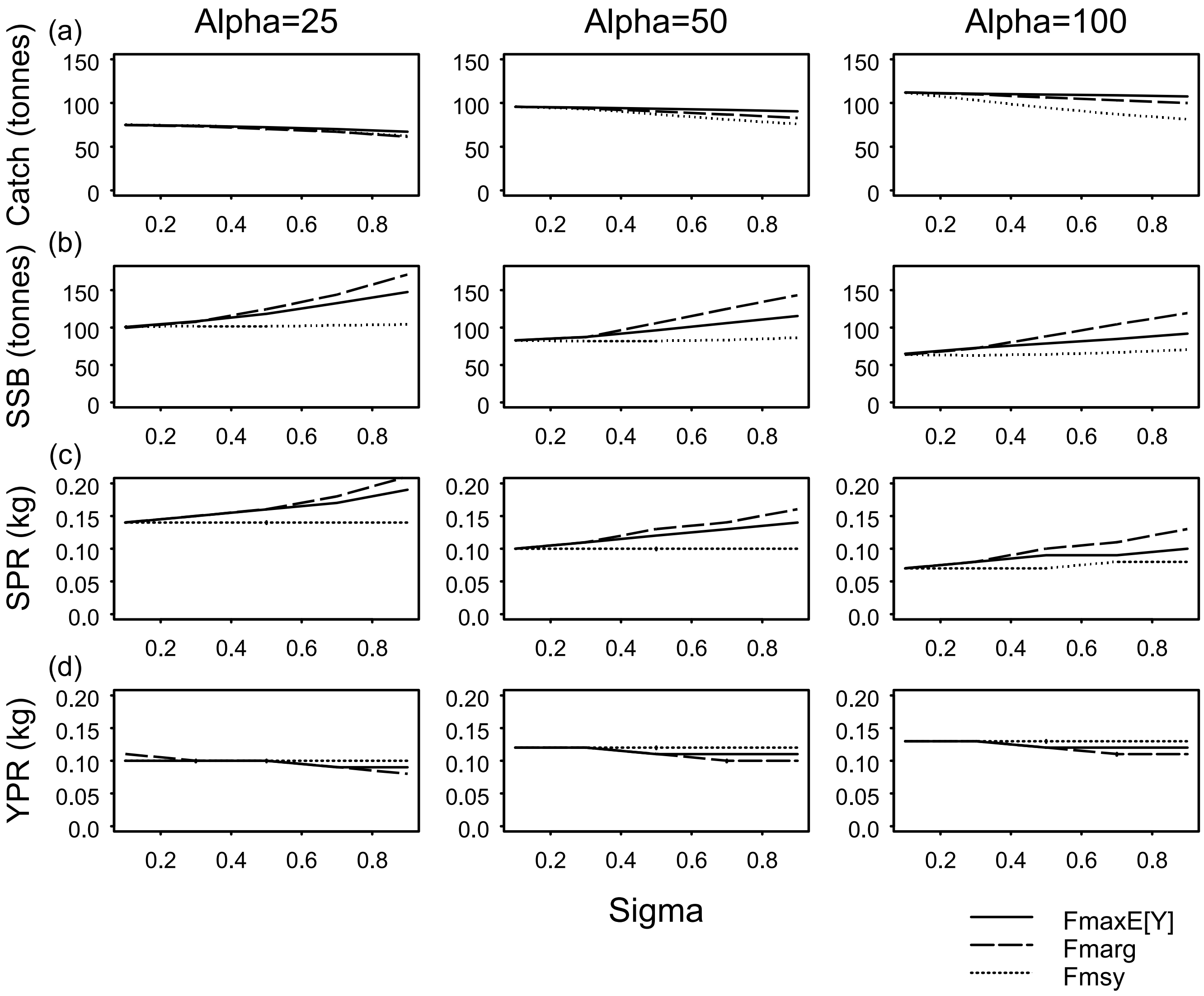
Alpha=25
Alpha=50
Alpha=100
(a)
Catch (tonnes)
(b)
SSB (tonnes)
(c)
SPR (kg)
(d)
YPR (kg)
0
50
100
150
0.0
0.05
0.10
0.15
0.20
0.2
0.4
0.6
0.8
Sigma
FmaxE[Y]
Fmarg
Fmsy

Figure 5.

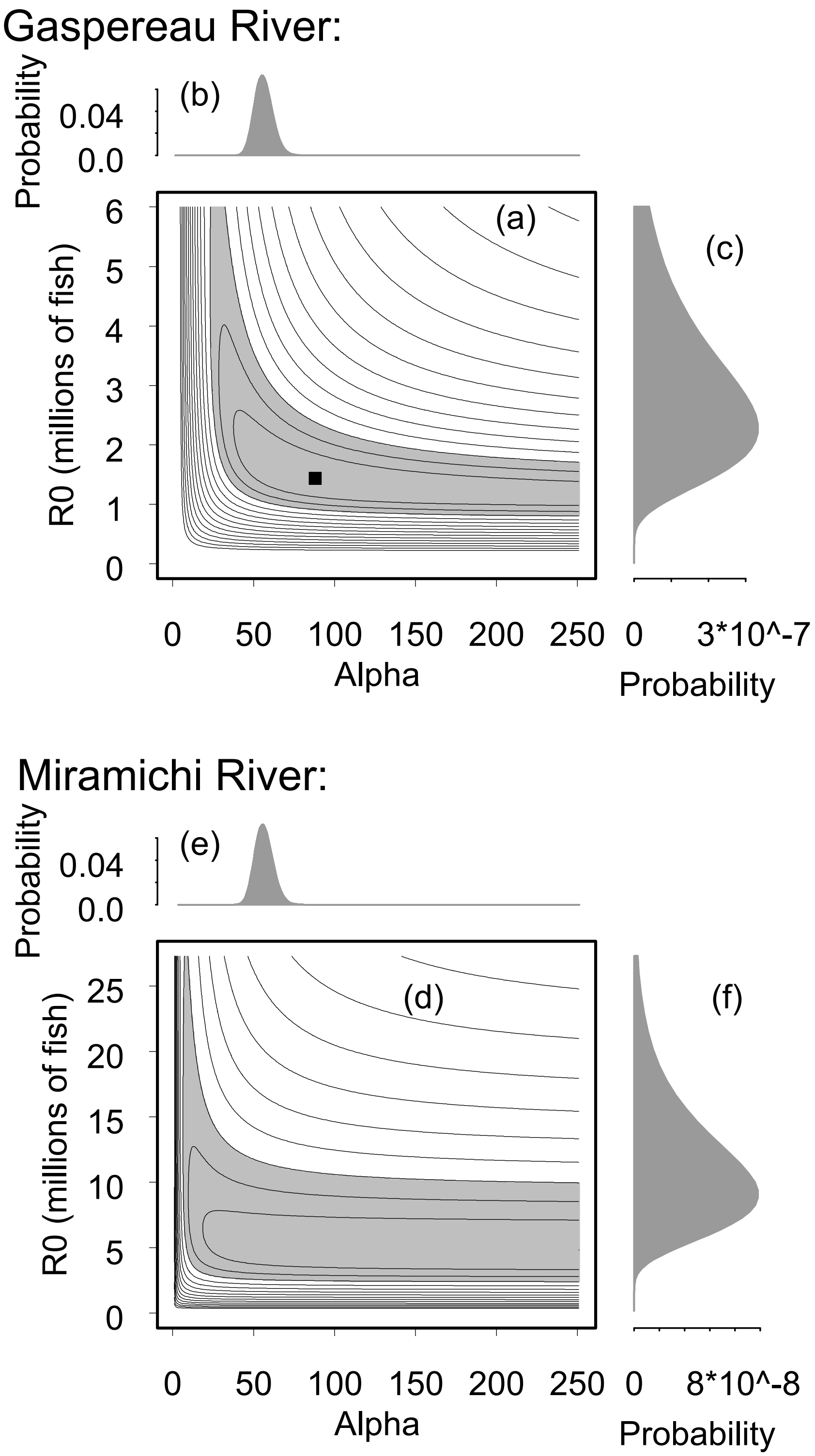
Gaspereau River:
Probability
(b)
0.04
0.0
(a)
R0 (millions of fish)
6
5
4
3
2
1
0
0
50
100
150
200
250
Alpha
(c)
0
3*10^-7
Probability
Miramichi River:
Probability
(e)
0.04
0.0
(d)
R0 (millions of fish)
25
20
15
10
5
0
0
50
100
150
200
250
Alpha
(f)
0
8*10^-8
Probability

Figure 6.