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The Maximum Reproductive Rate of Fish at Low Populations Sizes

by

Ransom A. Myers [1]
Killam Chair in Ocean Studies,
Department of Biology,
Dalhousie University,
Halifax, Nova Scotia,
Canada B3H 4J1,

K. G. Bowen, N. J. Barrowman
Dept. of Mathematics and Statistics,
Dalhousie University,
Halifax, Nova Scotia,
Canada B3H 4J1,

Gordon Mertz[2],
Department of Fisheries and Oceans
P.O. Box 5667, St. John's, NF A1C 5X1, Canada

Abstract

We examine the database of over 500 spawner-recruitment series compiled by Myers et al. (1995) to search for parameters that are constant, or nearly so, at the level of a species or above. We find that the number of spawners produced per spawner each year at low populations is relatively constant within species and that there is relatively little variation among species. This quantity can be interpreted as a standardized slope at the origin of a spawner-recruitment function. We employ variance components models that assume that the log of the standardized slope at the origin is a nor-

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[1] email - Ransom.Myers@Dal.Ca; telephone 1-902-494-1755

[2] My good friend Gordon Mertz tragically died while this manuscript was being finalized; his intelligence, humor and charm will be greatly missed – R.A. Myers

mal random variable. This approach allows improved estimates of spawner-recruitment parameters and the estimation of empirical prior distributions for Bayesian analysis.

Introduction

Perhaps the most fundamental parameter in population biology is the reproductive rate at low population size. We will analyze this parameter in terms of the maximum annual reproductive rate, which we define as the average rate replacement spawners are produced per spawner per year at low abundance (after a time delay for the age at maturity). The maximum annual reproductive rate is central to the estimation of the following:

- the population growth rate, i.e., "r", (Cole 1954; Pimm 1991; Myers et al. 1997).
- limits to overfishing (Mace 1994; Myers et al. 1994; Cook et al. 1997; Myers and Mertz 1998).
- the dynamic behaviour of the population, i.e. whether the population has oscillatory or chaotic behaviour.
- extinction models and population viability analysis (Lande et al. 1997).
- establishment of biological reference points for management. In some cases, e.g. the estimation of the maximum sustainable yield under the Ricker model, it suffices to determine the reference point.

The purpose of this paper is to provide a comprehensive analysis of this parameter in terms of a relatively simple statistical model, to attempt to determine under what conditions the parameter is invariant, e.g. constant for a species, and to provide empirical Bayesian priors for the estimates. We use the extensive database of stock and recruitment data compiled in Myers et al. (1995) and Myers and Barrowman (1996).

Formulation

Estimating Reproductive Rate

Semelparous species, whose members conveniently die after reproduction, immensely simplify the lives of students of the population biology of many insects and Pacific salmon of the genus *Oncorhynchus*. One generation follows the next in easy units, usually simply numbers. The relationship between the numbers in year t, N_t, and the numbers in year t plus the age at maturity, a_{mat}, is typically given in the form

$$N_{t+a_{mat}} = \alpha N_t e^{-f(N_t)}, \tag{1}$$

where the density-dependent mortality, $f(N_t)$, is a non-negative function such that $f(N_t) \to 0$ as $N_t \to 0$.

The dynamics of iteroparous species is more complicated. Typically, the number of recruits, R_t, is a function of the egg production or a proxy such as weight of spawners at time t, S_t, as in the form

$$R_t = \alpha S_t e^{-f(S_t)}, \tag{2}$$

where $f(S_t)$ is the density-dependent mortality as before.

We follow the usual convention in fisheries of assuming the number of eggs produced is proportional to the biomass of spawners. The Ricker model has the form

$$R_t = \alpha S e^{-\beta S_t}, \tag{3}$$

where α is the slope at the origin (measured perhaps in recruits per kilogram of spawners). Density-dependent mortality is assumed to be the product of β times the recruitment.

For the forthcoming calculations, the slope at origin, α, must be standardized. First consider

$$\hat{\alpha} = \alpha \cdot \mathrm{SPR}_{F=0}$$

where $\mathrm{SPR}_{F=0}$ is the spawning biomass resulting from each recruit (perhaps in units of kg-spawners per recruit) in the limit of no fishing mortality ($F = 0$). This quantity, $\hat{\alpha}$, represents the number of spawners produced by each spawner over its lifetime at very low spawner abundance. The quantity, $\tilde{\alpha}$, required for our calculations is the number of spawners produced by each spawner per year (after a lag of a years, where a is the age at maturity). If adult survival is p_s then $\hat{\alpha} = \sum_{i=0}^{\infty} p_s^i \tilde{\alpha}$, or summing the geometric series

$$\tilde{\alpha} = \hat{\alpha}(1 - p_s) = \alpha \cdot \mathrm{SPR}_{F=0}(1 - p_s)\ . \tag{4}$$

This quantity, $\tilde{\alpha}$ is the maximum annual reproductive rate, and will be the main focus of this study.

A word of warning is needed in the interpretation of the maximum annual reproductive rate. The above formulation is for the deterministic case. However, if stochastic variations in survival are included, then the quantity, $\tilde{\alpha}$, would be interpreted as the maximum of the average annual reproductive rate, e.g. the reproductive rate may be higher or lower for any given year.

The Ricker model provides a reasonable model for estimating the slope at the origin

The simplest form of density-dependent mortality is linear, i.e. $f(S) = \beta S$, in Eq. 1. We will show that under reasonable conditions this is perhaps the best first approximation. A simple generalization of the Ricker model is

$$f(S) = \beta S^{\gamma}, \tag{5}$$

where γ controls the degree of nonlinearity in the functional form of density-dependence (Bellows 1981). For most of the data sets there is not sufficient data to estimate γ; however, our purpose is only to insure that our estimates of α are robust to our assumptions about γ. We will examine data for cod because there is excellent data for these populations and all have been reduced to low levels, which will enhance our ability to estimate α. We held γ fixed at values of 0.5, 0.75, 1, 1.25, and 1.5 (Fig. 1 and 2) and estimated $\tilde{\alpha}$ and β. The functional fits are displayed *in terms of survival* ($\log(\frac{R}{S})$) versus S, where R has been multiplied by $\mathrm{SPR}_{F=0}(1 - p_s)$.

Fig. 1 near here
Fig. 2 near here

If $\gamma < 1$, then survival is a convex function of spawner biomass, and the limit of survival is infinity as $S \to 0$. Thus, this model is unrealistic for this case. Furthermore, an examination of the survival versus spawner curves reveals that this is often because of a completely unwarranted extrapolation beyond the lowest observed spawner abundance (Fig. 1). For $\gamma > 1$, survival is a concave function, and the derivative of survival as $S \to 0$ will always be zero.

In practice the Ricker model is a reasonably cautious estimate of the limit for management purposes. If $\gamma < 1$ is assumed, then a greater α is estimated, while the assumption of $\gamma > 1$ results in only a slight increase in the estimate of α (Fig. 1 and 2). If we examine the 4 cod populations with the largest range in observed spawner biomass, the estimate of the slope at the origin appears reasonable in all cases for the Ricker model, while the estimate for $\gamma = 0.5$ is inflated commensurately with the gap between the origin and the lowest observation of spawner abundance.

We also considered another common 3 parameter model, the "Shepherd Function", i.e.,

$$R = \frac{\alpha S}{1 + (S/K)^{\delta}} \tag{6}$$

This model was first proposed by Maynard Smith and Slatkin (1973) and was discussed by Bellows (1981). The parameter K has dimensions of biomass and may be interpreted as the "Threshold Biomass" for the model. For values of biomass S greater than the threshold K, density-dependent effects dominate. The parameter δ may be called the "degree of compensation" of the model, since it controls the degree to which the (density-independent) numerator is compensated for by the (density-dependent) denominator. If $\delta = 1$, then the Beverton-Holt model is recovered. However, for $\delta < 1$ survival is infinity as $S \to 0$; again, in this case the model cannot be considered as a reliable method to extrapolate to low population sizes. For $\delta > 1$, the derivative of survival as $S \to 0$ will always be zero. However, even if $\gamma = 1$, i.e. the Beverton-Holt model, then many estimates of the slope at the origin will be infinity. That is, if $K \to 0$, then $\alpha \to \infty$ is a perfectly feasible solution.

The Deriso-Schnute model (Hilborn and Walters 1992), an alternative 3 parameter model, has the Ricker and the Beverton-Holt as special cases. However, it suffers from the same problems we stated above: survival is not constrained to be finite except when the model is a Ricker model, or it has the derivative of survival as $S \to 0$ constrained to be zero.

Any estimation of the slope at the origin is necessarily an extrapolation since there can be no observations at zero spawner abundance. The simplest extrapolation is a linear one (in the relationship between log survival and spawner abundance), while alternative assumptions will often produce unreasonable estimates.

One situation in which a Ricker model would not give a precautionary estimate would be if mortality increased at low spawner abundances, known as depensation or the Allee effect. Myers et al. (1995) carried out a meta-analysis and could find no convincing evidence that depensation occurred for exploited fish populations. We conclude that the estimate of α from the Ricker model is a reasonable precautionary limit.

In this section we have argued that the Ricker model is often a reasonable model for the estimation of the $\tilde{\alpha}$ (some alternative approaches are discussed below). For the cod populations in the North Atlantic we have seen that the estimates are only slightly modified if survival is a concave function of spawner biomass. The alternative assumption, that log survival is a convex function, which usually results in the assumption that survival greatly increases at low spawner biomass (Fig. 1) is not strongly supported by the data and may be very dangerous for management decisions in extrapolations to low abundance.

Estimation Method

Variance Components Models

Our contention is that focusing on one population at a time can be misleading. In this section we shall demonstrate how this can be avoided by incorporating the estimation of the Ricker model into a standard linear mixed model. This can then easily be estimated using widely available software, e.g. SAS or SPLUS.

We will change notation slightly so that our results are directly in the standard notation of variance components and mixed models. We consider p populations, subscripted by i, for each of which we want to estimate a model of the form

$$\log \frac{R_{i,t}}{S_{i,t}} = \log \tilde{\alpha}_i + \beta_i S_{i,t} + \varepsilon_{it}, \qquad (7)$$

where we assume that $\log \tilde{\alpha}_i$ is a normal random variable, i.e. a random effect. We define $a_i \equiv \log \tilde{\alpha}_i$.

We consider the log survival, $\log \frac{R}{S}$, of a yearclass from a given population as an element of a vector $\mathbf{y}$. If there are n_i observations for population i, then the first n_1 elements of the vector $\mathbf{y}$ will be the n_1 log survivals for the first population, followed by the n_2 log survivals for the second population, and so on.

We consider the fixed effects of the model first. In our case, the parameters we estimate are the overall mean, μ, for the model and p regression parameters, β_i. We consider the spawner abundances, $S_{i,t}$, as known, and will estimate the density-dependent regression parameter, β_i, for each population. By happy coincidence, the standard mixed model notation for the vector of fixed effects parameters is $\boldsymbol{\beta}$. The unknown vector $\boldsymbol{\beta}$ consists of the overall mean, μ, and the p β_i's. The vector $\boldsymbol{\beta}$ is related to $\mathbf{y}$ by the known model matrix $\mathbf{X}$, whose elements are 0, 1, and $S_{i,t}$; the form of this matrix is given below.

We will let the log of the slope at the origin, a_i, be an unknown random effect that is constant for each population, i.e. they are assumed to be drawn from a normal distribution with variance that is estimated in the model. We shall use the standard mixed model notation for the unknown vector of random effects $\mathbf{u}$, whose elements will be a_i. The vector $\mathbf{u}$, is related to the $\mathbf{y}$ by a known model matrix $\mathbf{Z}$; the form of $\mathbf{Z}$ is given below.

In standard mixed model notation, we have:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \boldsymbol{\epsilon} \qquad (8)$$

Here, $\boldsymbol{\epsilon}$ is an unknown random error vector. For example, consider the simple case of two populations, each of which are observed for three years and the first year is denoted as 1. The above equation can then be written as

$$\mathbf{y} = \begin{bmatrix} y_{11} \\ y_{12} \\ y_{13} \\ y_{21} \\ y_{22} \\ y_{23} \end{bmatrix} = \begin{bmatrix} 1 & S_{11} & \cdot \\ 1 & S_{12} & \cdot \\ 1 & S_{13} & \cdot \\ 1 & \cdot & S_{21} \\ 1 & \cdot & S_{22} \\ 1 & \cdot & S_{23} \end{bmatrix} \begin{bmatrix} \mu \\ \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} 1 & \cdot \\ 1 & \cdot \\ 1 & \cdot \\ \cdot & 1 \\ \cdot & 1 \\ \cdot & 1 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} \epsilon_{11} \\ \epsilon_{12} \\ \epsilon_{13} \\ \epsilon_{21} \\ \epsilon_{22} \\ \epsilon_{23} \end{bmatrix} \tag{9}$$

where $y_{i,t} = \log \frac{R_{i,t}}{S_{i,t}}$. The generalization provided by the mixed model enables one not only to model the mean of $\mathbf{y}$ (as in the standard linear model), but to model the variance of $\mathbf{y}$ as well. We assume that $\mathbf{u}$ and $\boldsymbol{\epsilon}$ are uncorrelated and have multivariate normal distributions with expectations $\mathbf{0}$ and variances $\mathbf{D}$ and $\mathbf{R}$, respectively. The variance of $\mathbf{y}$ is thus

$$\mathbf{V} = \mathbf{Z}\mathbf{D}\mathbf{Z}' + \mathbf{R} \tag{10}$$

Note that when $\mathbf{R} = \sigma^2\mathbf{I}$ and $\mathbf{Z} = \mathbf{0}$, the mixed model reduces to the standard linear model.

One can model the variance of the data, $\mathbf{y}$, by specifying the structure (or form) of $\mathbf{D}$ and $\mathbf{R}$. In the simplest case one might assume that the error variance is the same for all populations, i.e. $\mathbf{R} = \sigma^2\mathbf{I}$. However, we estimate a separate estimation error variance for each population, σ_i^2. We also test if the residuals are autocorrelated. If they are, we estimate a separate autocorrelation parameter, ρ_i, for each population. This results in a block diagonal structure for $\mathbf{R}$.

Now that we have transformed the problem into this form, estimation is trivial because high quality software exists for this problem (Appendix A).

The likelihood function for the data vector $\mathbf{y} \sim \mathcal{N}_N(\mathbf{X}\boldsymbol{\beta}, \mathbf{V})$ is

$$L = L(\boldsymbol{\beta}, \mathbf{V}|\mathbf{y}) = \frac{e^{-\frac{1}{2}(\mathbf{y}-\mathbf{X}\boldsymbol{\beta})'\mathbf{V}^{-1}(\mathbf{y}-\mathbf{X}\boldsymbol{\beta})}}{(2\pi)^{\frac{1}{2}N}|\mathbf{V}|^{\frac{1}{2}}}. \tag{11}$$

There are two common approaches to analyze this function: maximum likelihood (ML) and restricted maximum likelihood (REML) (Searle et al. 1992). REML differs from ML for this model in that it takes into account the degrees of freedom used for estimating the fixed effects, whereas ML does not. Furthermore, in the case of balanced data REML solutions are identical to ANOVA estimators which have known optimality properties. For these reasons, we will use REML, but will consider ML for robustness.

Estimation and prediction of individual population parameters

The use of mixed models allows us to obtain improved estimates of parameters for any one population. In general we not only wish to estimate the model parameters, we wish to predict the random variables for each population. In our case we wish to estimate the density-dependent parameter β

and predict the slope at the origin, which is assumed to be a random variable, for each population. To obtain the Best Linear Unbiased Predictors (BLUP) we need the mixed model equations

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z}+\mathbf{D}^{-1} \end{bmatrix} \begin{bmatrix} \tilde{\beta} \\ \tilde{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix} \qquad (12)$$

Where we use $\tilde{}$ to represent solutions.

Without the $\mathbf{D}^{-1}$ in the lower right-hand submatrix of the matrix on the left, they would be the ML equations for the model treated as if $\mathbf{u}$ represented fixed effects, rather than random effects. Although the above equation has been discussed in terms of classical methods, the same result is arrived at using a formal Bayes analysis of incorporating prior information into the analysis of data (Searle et al. 1992).

Our estimation methods above provide estimates of a_i, i.e. $\log \tilde{\alpha}_i$. To obtain estimates of the $\tilde{\alpha}_i$, exponentiate the estimate of a_i and multiply by $e^{\frac{1}{2}\sigma_\epsilon^2}$, where σ_ϵ^2 is the square of the standard error of a_i.

Data sources and treatment

The data we used are estimates obtained from assessments compiled by Myers et al. (1995). For marine populations, population numbers and fishing mortality were estimated using sequential population analysis (SPA) of commercial catch at age data for most marine populations. SPA techniques include virtual population analysis (VPA), cohort analysis, and related methods which reconstruct population size from catch at age data (see Hilborn and Walters (1992), chapters 10 and 11, for a description of the methods used to reconstruct the population history). Briefly, the commercial catch at age is combined with estimates from research surveys and commercial catch rates to estimate the numbers at age in the final year, and to reconstruct previous numbers at age under the assumption that commercial catch at age is known without error and that natural mortality at age is known and constant.

For Pacific salmon stocks, spawner abundance is the estimate of the number of upstream migrants discounted for mortality within the river and recruitment combines catch and the number of upstream migrants.

SPA techniques were used for the freshwater species except for brook trout. The 7 brook trout populations were from introduced populations in California mountain lakes (DeGisi 1994); these populations were estimated using research gillnets and maximum likelihood depletion estimation.

Time series of less than 10 years are not included in this analysis. The $\text{SPR}_{F=0}$ was calculated using estimates of natural mortality, weight at age, and maturity at age. Maturity and weight at age were usually estimated from research surveys carried out for each population.

A major source of uncertainty in the SPA estimates of recruitment and spawning stock biomass (SSB) is that they usually assume that catches are known without error. This is particularly important when estimates of discarding and misreporting are not included in the catch at age data used in the SPA. These errors are clearly important for some periods of time for some of the cod stocks (Myers et al. 1997) and these errors will affect our estimates of the number of replacements each spawner can produce at low population densities ($\tilde{\alpha}$).

Results

We first estimated the maximum annual reproductive rate, $\tilde{\alpha}_i$, individually for each population using a standard Ricker model fit (Fig. 3, Table 1). We then used the mixed model to estimate the true variability among populations in the the maximum annual reproductive rate. As expected, the estimate of the true variability in the maximum annual reproductive rate is much less than the sample variability because individual estimates contain estimation error. For example, for pink salmon, if $\tilde{\alpha}$ is estimated separately for each stock, then there is a order of magnitude range of the estimates. However, if $\tilde{\alpha}$ is assumed to be a random variable, then the mixed model estimates suggests that the true range is very small, with all the true values being very close to 3 (Fig. 3). Cod show a similar story. The number of replacement spawners per spawner per year for cod at low abundance is between 3 and 4; resulting in a maximum net reproductive rate (if there is no fishing mortality) of between 15 and 20. The maximum annual reproductive rate for herring appears to be slightly less, and for hakes of the genus *Merluccius*, e.g. silver hake and Pacific hake, is around 1. Some anadromous species, e.g. sockeye salmon, appear to have a maximum annual reproductive rate of around 4 or 5, while others, e.g. pink salmon, have a much lower rate.

Fig. 3 near here

The most remarkable aspects of the results is the relative constancy of the estimates of the maximum annual reproductive rate. The log of the maximum reproductive rate is almost always close to one for the species with more than one population in our analysis (Fig. 5a). For the species with multiple populations only Pacific Ocean perch and silver hake have a maximum annual reproductive rate less than 1; all other species have estimates that range between 0.2 and 1.6 (all of these numbers will be inflated when the estimates are converted to a linear scale from the log scale).

Fig. 5 near here

We believe that the low estimates for Pacific Ocean perch are probably associated with its very low adult natural mortality. Its maximum lifetime annual reproductive rate is around 3 (Fig. 6a). This value is low compared to other species, which suggests that it should be harvested much more cautiously than other species.

Fig. 6 near here

The estimates of the maximum annual reproductive rate for species for which we have only one population are much more variable than the species with many populations (Fig. 5b. and 6b). The greater variability in these estimates is at least partially caused by estimation error. However, several species have maximum reproductive rates that suggest that they cannot sustain intense fisheries. In some cases this is certainly true. The southern bluefin tuna in the Southern Ocean and the pelagic armourhead on the Southeast Hancock Seamount were both greatly reduced by overfishing. In other cases, there may be serious problems with the assessments. For example, the grey mullet has supported a fishery around Taiwan for many years, so it is unlikely that the true maximum reproductive rate is as low as we estimated.

Despite the large variation in the individual estimates, our general conclusion about the relative constancy of the maximum annual reproductive rate stands, the estimates are usually around 3.

There are exceptions for individual stocks, but these usually have large standard errors.

In order to make our individual and mixed model analysis comparable, we used a first order autocorrelated error assumption for the species if an autocorrelated error model was needed for populations of the species. We used this assumption for cod, (Fig. 4).

We next estimated the mean and variance of $\log \tilde{\alpha}$ for each species for which there was sufficient data, and finally the predicted value of each $\log \tilde{\alpha}$ under the mixed model.

Note that there is less variance in the BLUP numbers from the traditional estimates (Fig. 4). The estimates with relatively few data points, e.g. Gulf of Maine cod, are pulled towards the overall mean more than those populations with many years of data, e.g. Iceland cod.

Fig. 4 near here

Note that herring has a smaller maximum reproductive rate than many species. The lower mean is due to a few stocks in the northern north Atlantic which have been reduced to very low levels (the Iceland stocks, the Norway (often called the "Arcto-Norwegian") stock, and the Georges Bank stocks).

Limitations and Alternative Approaches

The approach we have described here has many advantages, but researchers should be aware of the limitations of the approach, and alternative approaches.

The first limitation is the functional form assumed for density-dependent mortality. The Ricker model, and the nonlinear Ricker model (Eq. 5), used here is not appropriate for some species. For example, we did not consider coho salmon (*Oncorhynchus kisutch*) in this analysis because there the shape of the spawner recruitment curve was clearly asymptotic, similar to a Beverton Holt function. We will consider nonlinear mixed models in a future paper using the methods of Lindstrom and Bates (1990).

Second, we have also assumed that the distribution of the $\tilde{\alpha}$ is approximately lognormal. This distribution appears to be a reasonable approximation in most cases considered here, but violations of the assumption may cause biases (Verbeke and Lesaffre 1996).

A third assumption is that the model residuals are lognormal. This is by far the most common assumption used in fitting spawner recruitment models (Hilborn and Walters 1992); however, it may not always be the most appropriate assumption. The gamma distribution appears to give more reasonable fits to some stock recruitment data (Myers et al. 1995).

A fourth assumption is that all populations within a taxon are comparable, i.e. the maximum reproductive rate for populations within a species (or higher taxon) is described by a lognormal distribution. However, this parameter may vary in a systematic way among populations, e.g. populations in colder conditions may have a lower maximum reproductive rate. Such hypotheses can be investigated by letting the maximum reproductive rate be a random variable whose mean is a function of an exogenous variable, e.g. temperature.

If any of the above four assumptions appear to be seriously violated, then an alternative approach is needed. Perhaps the most convenient alternative framework to construct this type of model is either a Bayes or empirical Bayes hierarchical model (Efron 1996). Punt and Hilborn (1997) have recently reviewed these approaches in fisheries management. McAllister (1994) implement an empirical Bayes approach to estimating a parameter functionally related to the slope at the origin, e.g. the steepness parameter, using an earlier version of the data set used here.

The maximum likelihood estimators that we have used to estimate the underlying distribution of annual reproductive rates may result in estimates that are less "heavy tailed" than they should be (Efron 1996).

It should be remembered that this analysis does not get rid of known biases, e.g. estimation error in spawner abundance and time-series bias, in the treatment of spawner recruitment relationships, see Hilborn and Walters (1992) for a review.

Discussion

The analysis presented in this paper suggests a new and unsuspected finding: the maximum annual reproductive rate for any of the species examined is typically between 1 and 6. This number may be less for some species and more for others, but the relative constancy of the annual reproductive rate is an unanticipated, and very important, finding.

This analysis is consistent with our preliminary analysis (Myers et al. 1996); but was an unsuspected finding. For example, the common belief that there is no relationship between spawner biomass and recruitment is founded on the notion that the maximum reproductive rate for fish is essentially infinite (this belief is based upon the observation that fecundity of fish is often large). This erroneous belief is caused by the lack of attention paid to the information content of different data sets (Myers and Barrowman 1996; Myers 1997).

Hypotheses

This broad generalization demands an explanation. First, consider the lower limit of the annual reproductive rate at low abundance. This represents the "average" value that should occur at low abundance. Clearly, if this value is much less than 1, then the population may very well go extinct because the value would probably be below one for considerable lengths of time because of variation in the environment.

Why then would the annual reproductive rate be bounded at the upper end? A reasonable, but speculative, answer is that a very high value of the reproductive rate would imply an excess of resources that are not exploited. In this case, other competitors would be expected to evolve to exploit these resources.

Reducing Uncertainty

The uncertainty of the biological processes underlying the population dynamics of exploited species can be greatly reduced by combining data from many studies. The relative constancy of the maximum reproductive rate allows for simple, broad conclusions to be reached on the management of fish stocks. That the maximum reproductive rate is typically around 1 to 6 replacement spawners per spawner per year is a powerful tool for the management of fish stocks. It allows the maximum exploitation rate to be quickly estimated (Myers and Mertz 1998), and the recovery rates of exploited fish populations to be calculated (Myers et al. 1997).

Many of the crucial parameters needed for fisheries management can be estimated using the the maximum reproductive rate analyzed here, and the simple approximations, see (Myers and Mertz 1998; Myers et al. 1997). All that is required to use these approximations is data on natural mortality, age at maturity, and the maximum reproductive rate. These approximate formulas will require testing and verification, but this approach should allow progress to be made on critical issues. Thus, even if the maximum reproductive rate is not known for a species, the estimates complied in this paper allow them to be approximated, or our estimates can be used as priors in a Bayesian analysis.

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Appendix: Estimation in SAS

This appendix demonstrates how to fit the proposed model to data for a single species. In the SAS data step, a dataset is created with 3 variables per observation: the name of the stock (i.e. population), `stock`, the number or biomass of spawners, `s`, and the survival, `surv`, respectively. The survival is $\log(R/S)$, where recruitment, R, has been multiplied by $\mathrm{SPR}_{F=0}(1-p_s)$, so we will obtain estimates of $\tilde{\alpha}$, in the appropriate units.

The SAS code for fitting the model with autocorrelated recruitment is

```
proc mixed method=reml;
   class stock;
   model surv= s*stock /solution;
   random int /subject=stock;
   repeated /subject=stock group=stock type=AR(1);
```

This model assumes autocorrelated errors, and fits a separate first-order autocorrelation parameter and error variance are fit for each stock.

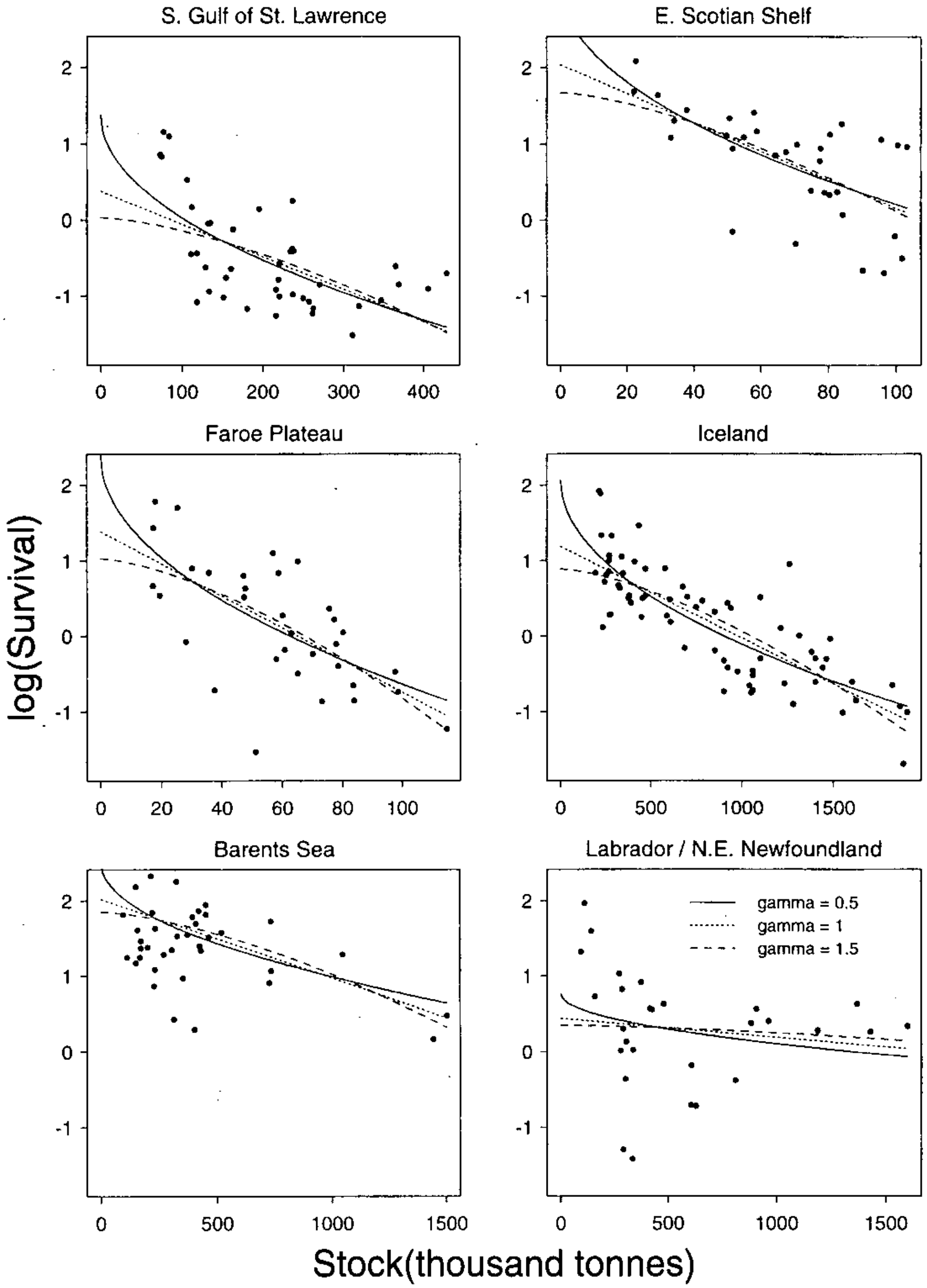


Fig. 1. Survival, $\log(\frac{R}{S})$, versus spawner abundance for 6 cod stocks. The modeled density-dependent mortality of the form $f(S) = \beta S^{\gamma}$ is shown for $\gamma = 1.5$, $\gamma = 1$, and $\gamma = 0.5$. We have standardized recruitment by multiplying by $\mathrm{SPR}_{F=0}(1 - p_s)$, which allows survival to be interpreted as the annual replacement of spawners per spawner. Thus, the intercept of the fitted curves provide an estimate of $\log \tilde{\alpha}$, i.e. the log of the maximum annual reproductive rate.

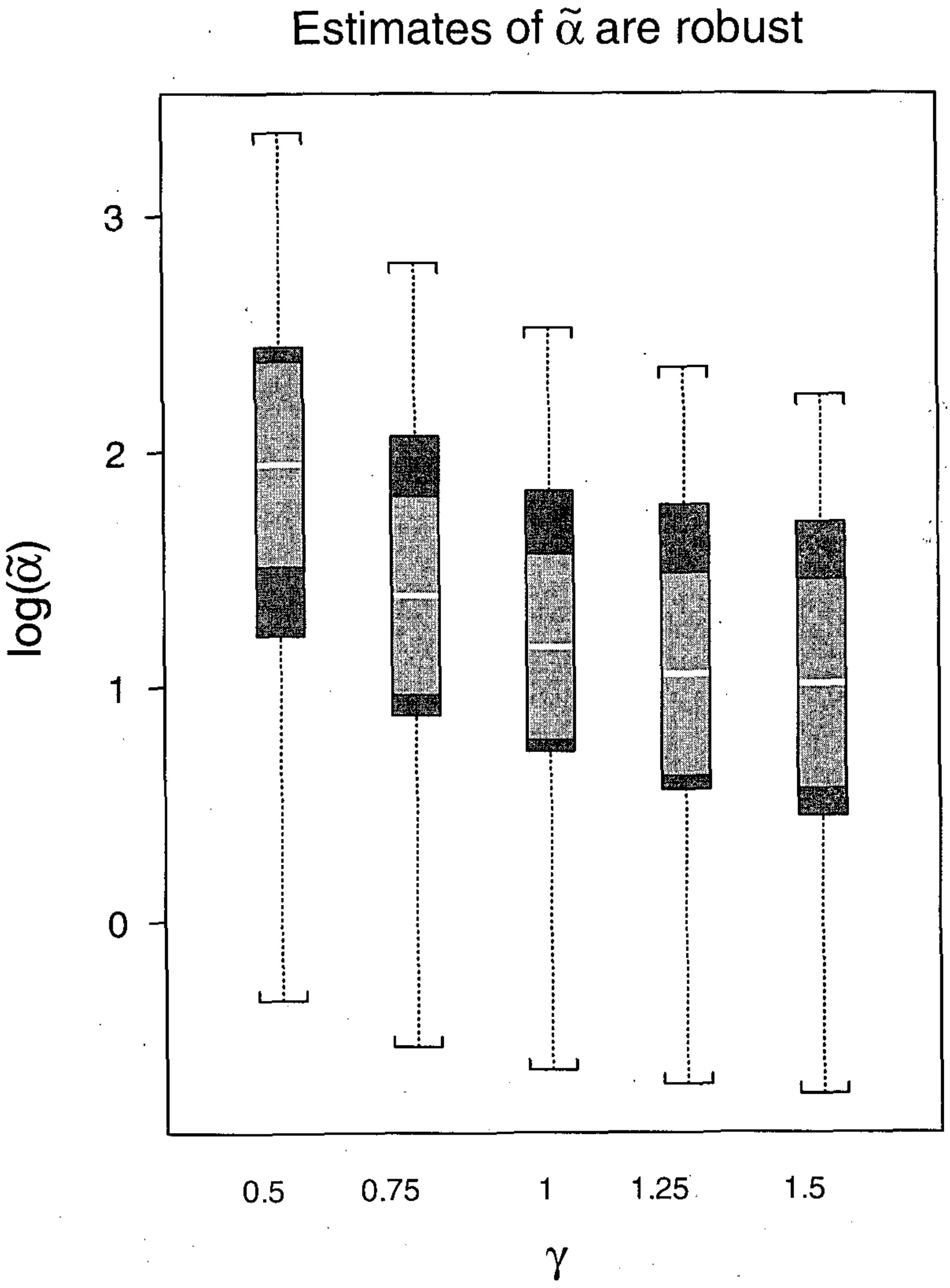


Fig. 2. Box plots of the log of the scaled slope at the origin, log($\tilde{\alpha}$) for the twenty major cod stocks in the North Atlantic as a function of the form of density-dependent mortality $f(S) = \beta S^{\gamma}$. When $\gamma = 1$ the Ricker model is recovered.

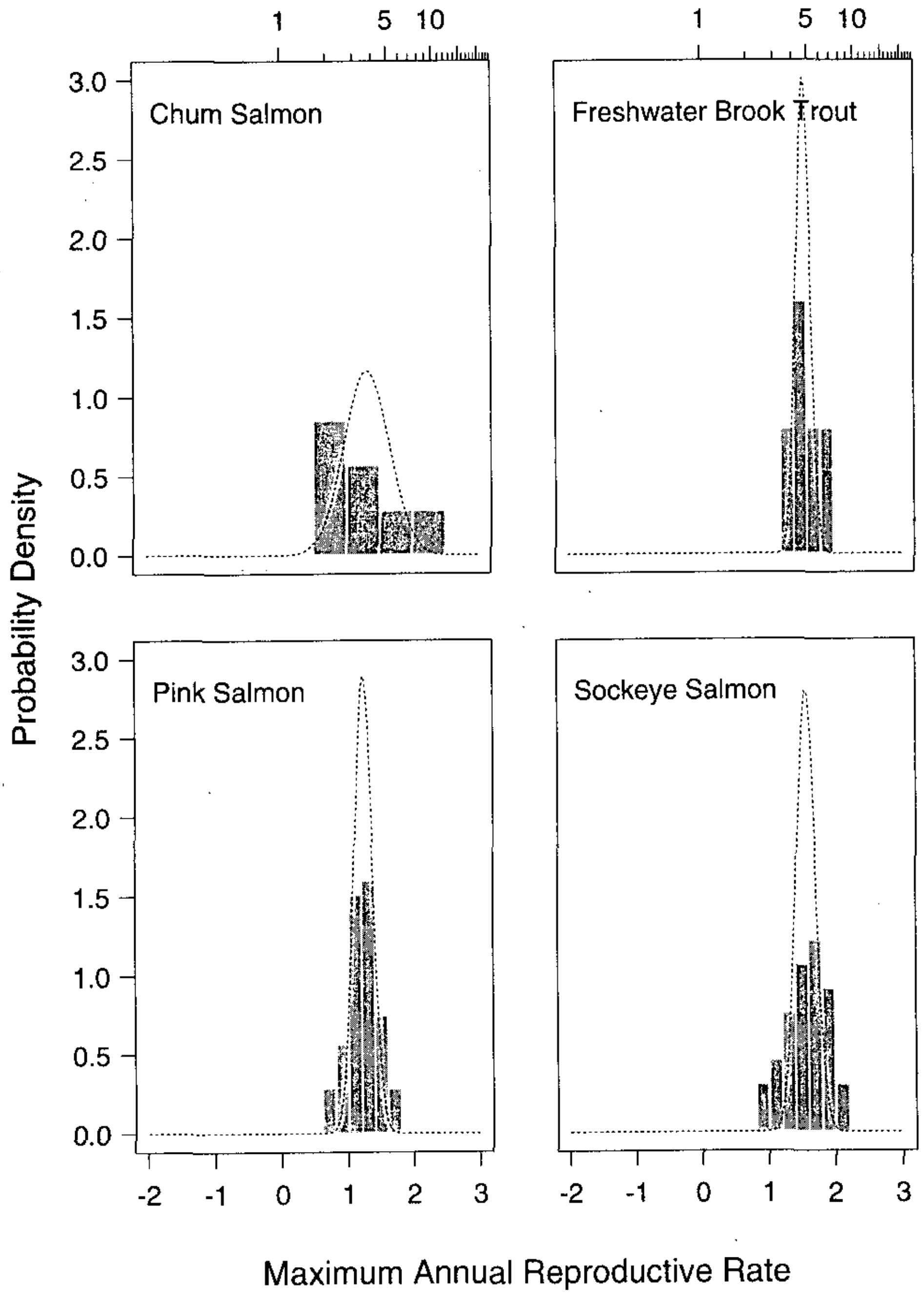
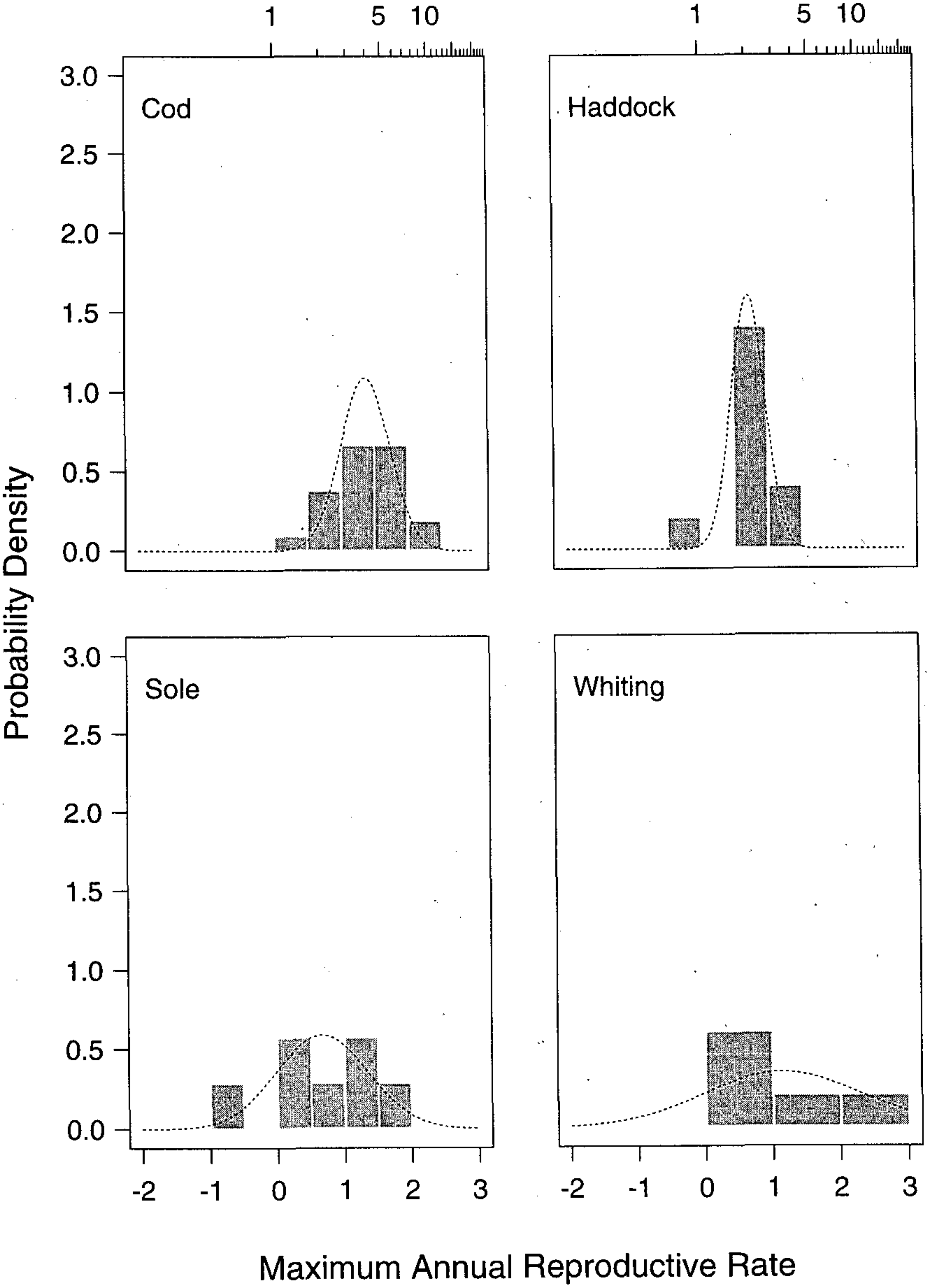


Fig. 3. Histograms of the individual maximum likelihood estimates of the log of the maximum annual reproductive rate compared with restricted maximum likelihood estimates of the true variability in the log of the annual reproductive rate, log($\hat{\alpha}$) from our mixed model analysis (solid line). The estimates for each individual population show a much wider variability because these estimates include the estimation error from each maximum likelihood fit. We can estimate the variability of the true underlying distribution because we can estimate the estimation error variance. Note that the top axis of the plots shows the untransformed annual reproductive rate.


1
5
10
1
5
10
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Cod
Haddock
Probability Density
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Sole
Whiting
-2
-1
0
1
2
3
-2
-1
0
1
2
3
Maximum Annual Reproductive Rate

- fig 4

R 3b

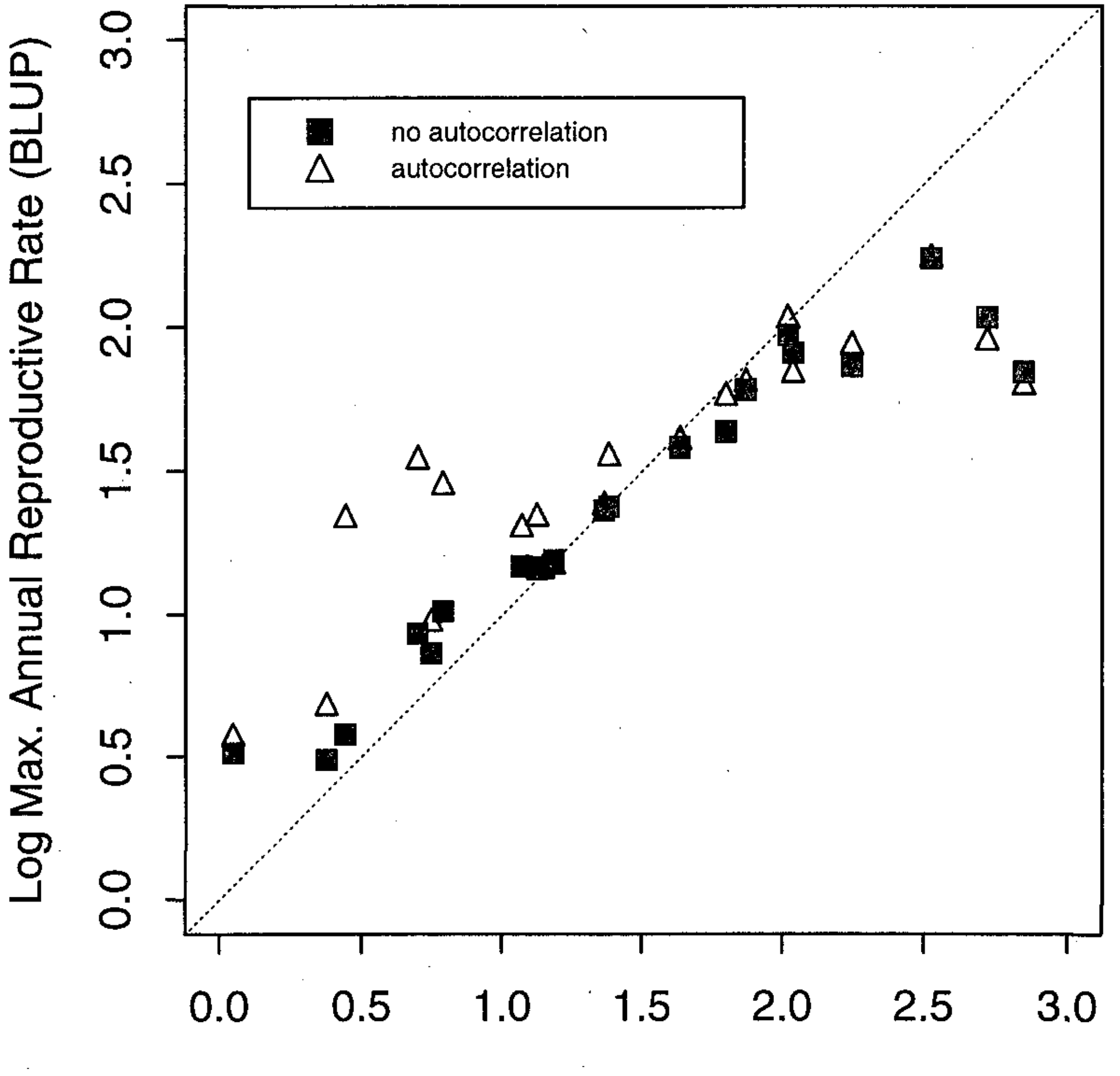


Fig. 4. A comparison of the annual reproductive rate $\log(\tilde{\alpha})$, obtained from independent regressions on each population, with the Best Linear Unbiased Predictors (BLUP) obtained for two different mixed models, one of which includes autocorrelation in the serial error structure. Data are for cod populations in the North Atlantic.

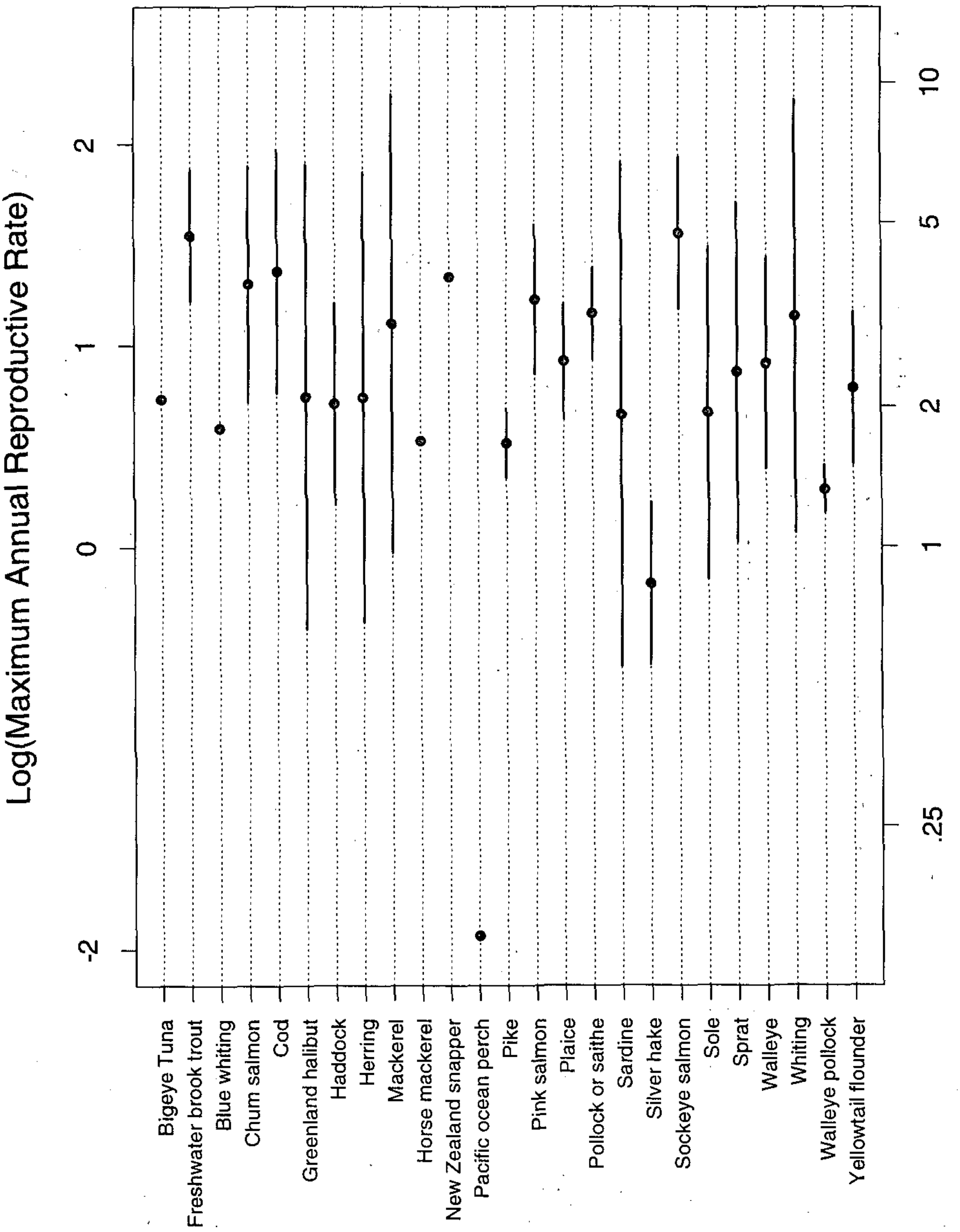


Fig. 5a. Estimates of the log of the maximum annual reproductive rate for species with multiple populations, where the error bars represent the estimated standard deviation of the log of the maximum annual reproductive rate (this estimate is sometimes zero if only two or three populations are sued in the analysis).

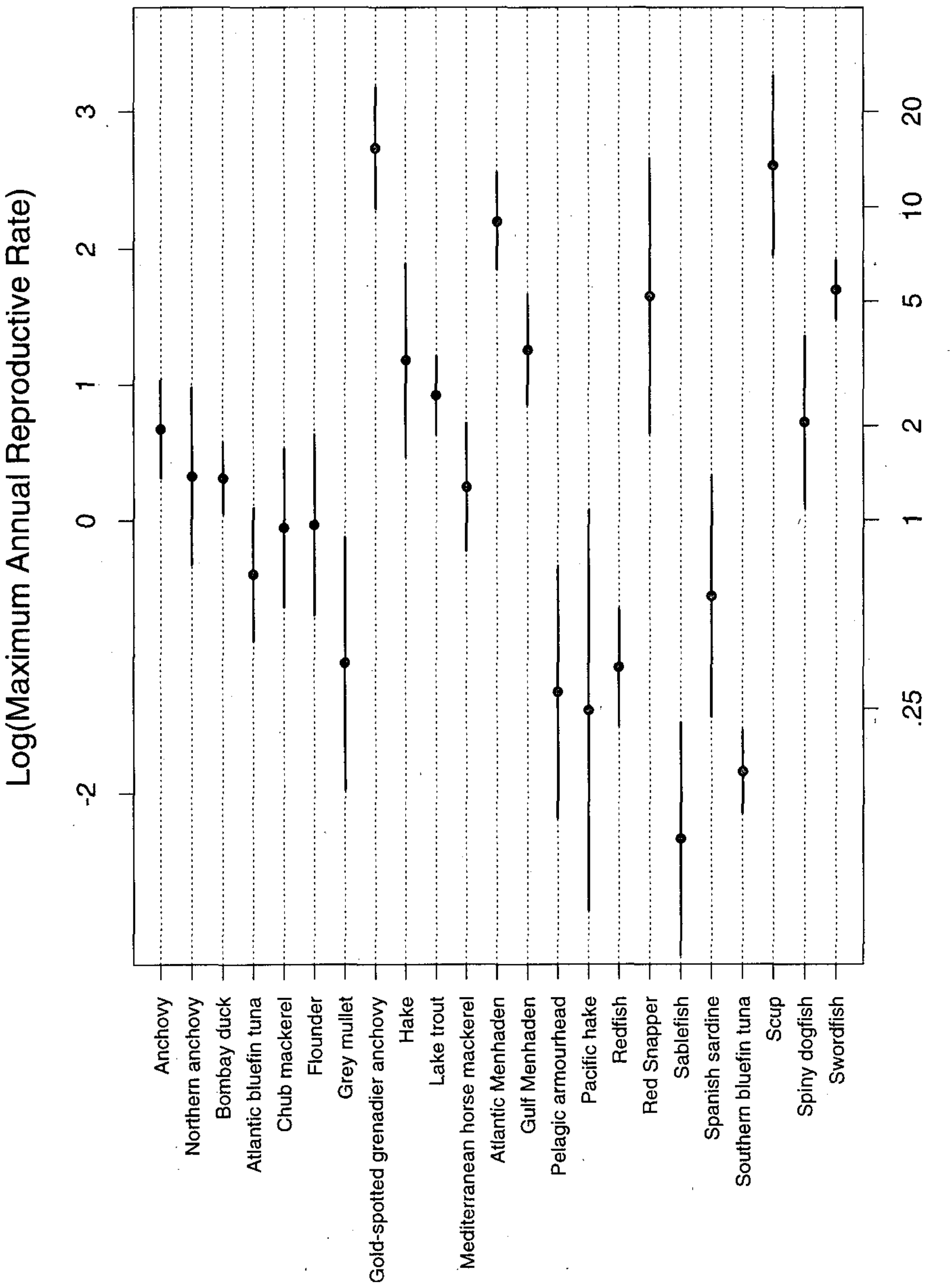


Fig. 5b Same as above but for species with only one population in the database, where the error bars represent the standard error of the estimate.

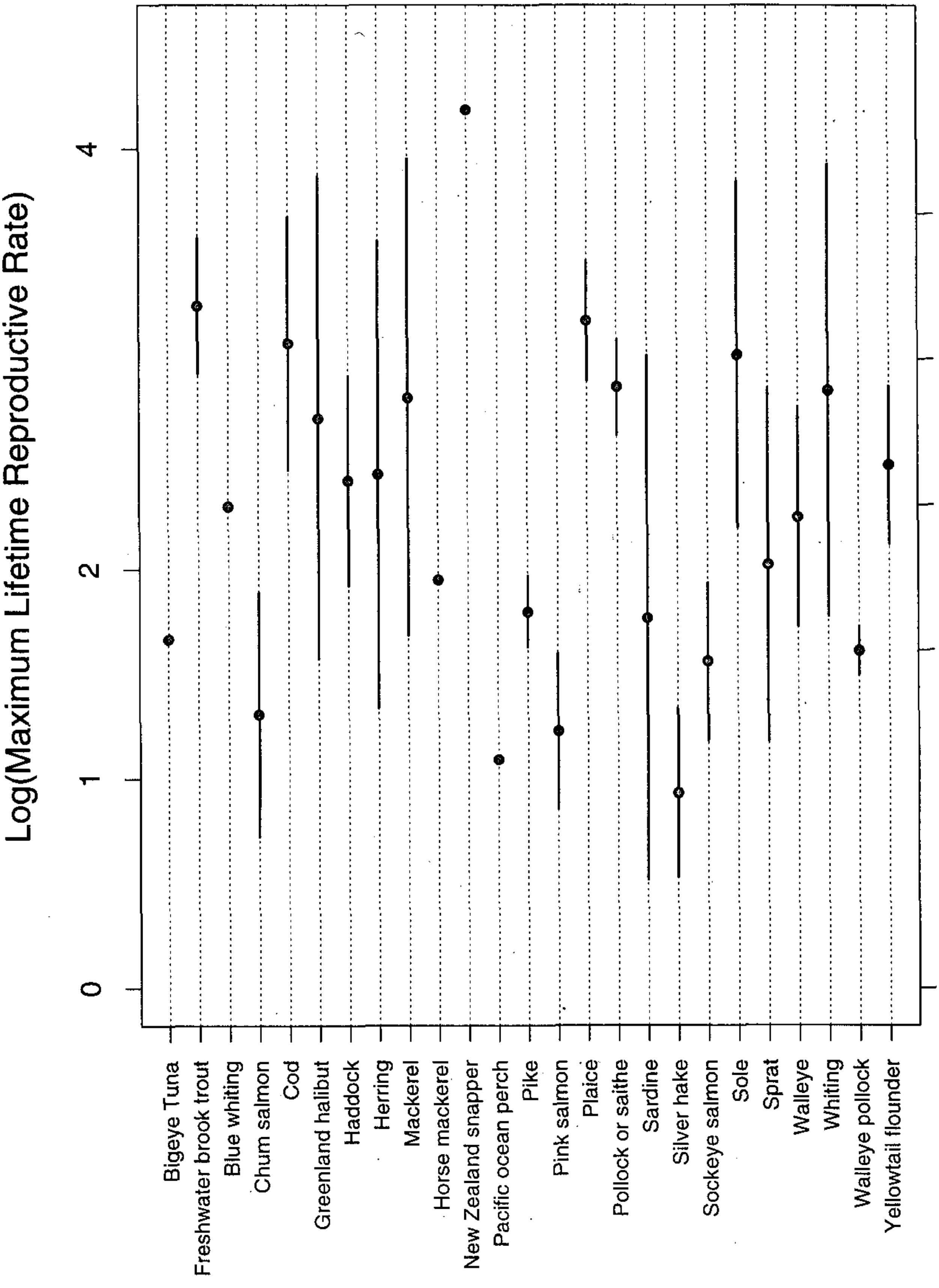


Fig. 6a. Estimates of the log of the maximum lifetime reproductive rate for species with multiple populations, where the error bars represent the estimated standard deviation of the log of the maximum lifetime reproductive rate; **b** species with single populations, where the error bars represent the standard error of the estimate.

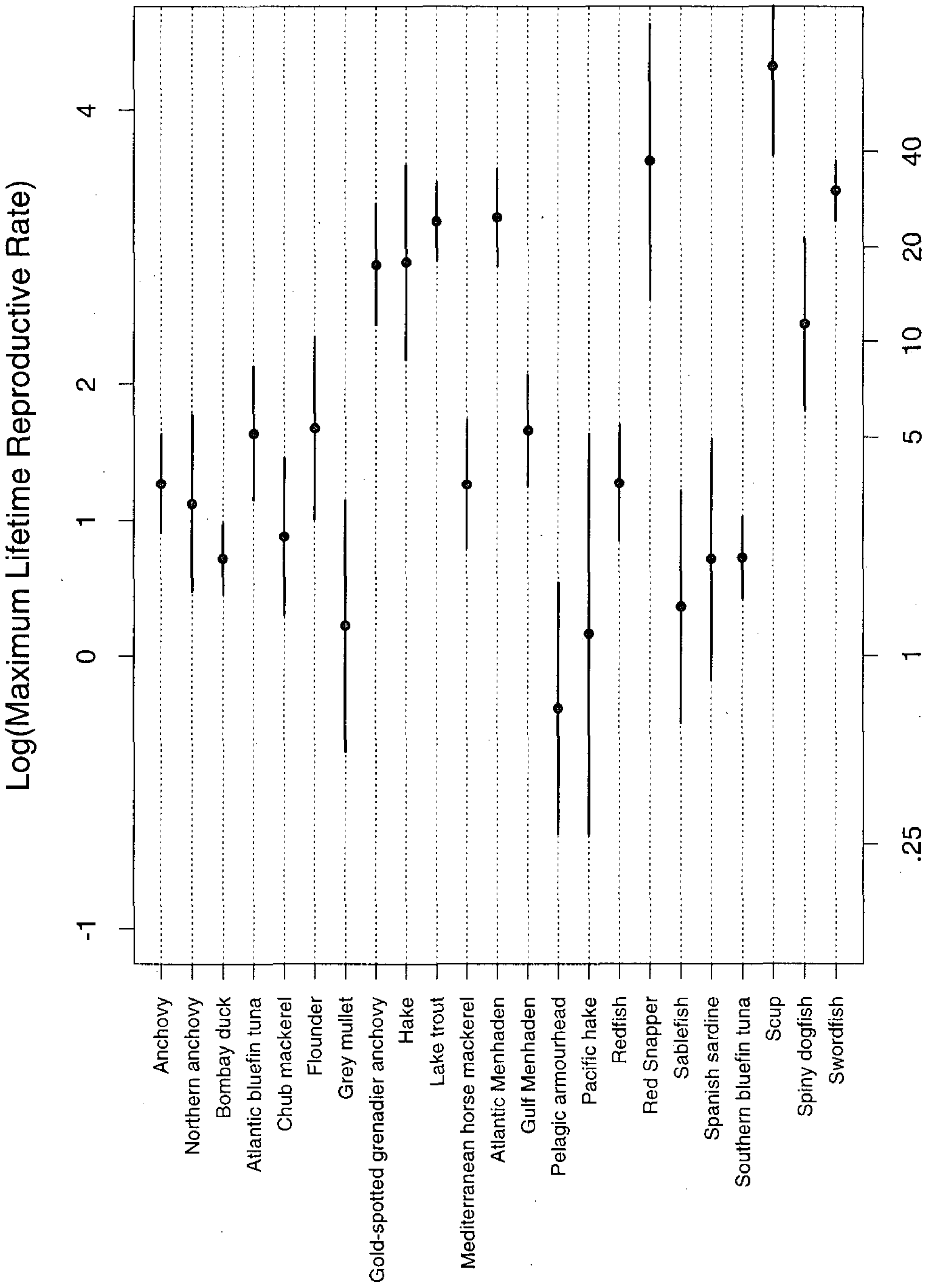


Fig. 6b Same as above but for species with only one population in the database, where the error bars represent the standard error of the estimate.