# **Depensation in fish stocks: a hierarchic Bayesian meta-analysis**

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**Abstract**: The probability of different levels of depensation within four taxonomic groups was calculated using a Bayesian technique called hierarchical modeling. With this method we combined spawner–recruit data from many stocks within a taxon to estimate the distribution describing the variability of depensation within that taxon. The spawner–recruit model we use allows for both depensation (lower than expected recruits at low population levels) and hypercompensation (where recruits are higher than expected at low population levels). The end product of our analysis is a probability distribution that can be used as a Bayesian prior when analyzing a new data set. We examined four taxonomic groups (the salmonids, gadiforms, clupeiforms and pleuronectiforms) and found that, for all of the taxa, the most likely values fell close to or within the range of no depensation. However, because the distributions were very broad we suggest that analysis of stock recruitment data should incorporate spawner–recruit curves that include the possibility of depensation and hypercompensation.

**Résumé** : La probabilité de différents degrés d'anticompensation à l'intérieur de quatre groupes taxinomiques a été calculée à l'aide d'une technique bayésienne appelée modélisation hiérarchique. Avec cette méthode, nous avons combiné les données reproducteurs-recrues provenant de nombreux stocks à l'intérieur d'un taxon pour estimer la distribution décrivant la variabilité de l'anticompensation à l'intérieur de ce taxon. Le modèle reproducteurs-recrues que nous avons utilisé tient compte à la fois de l'anticompensation (des recrues moins nombreuses que prévu à des niveaux de population faibles) et de l'hypercompensation (les recrues sont plus nombreuses que prévu à des niveaux de population faibles). Le produit final de notre analyse est une distribution de probabilités qui peut être utilisée comme une prémisse bayésienne dans l'analyse d'un nouvel ensemble de données. Nous avons examiné quatre groupes taxinomiques (des salmonidés, des gadiformes, des clupéiformes et des pleuronectiformes). Nous avons constaté que pour tous ces taxons, les valeurs les plus vraisemblables étaient proches ou à l'intérieur de l'étendue de non-anticompensation. Toutefois, parce que les distributions étaient très étendues, nous avons proposé que l'analyse des données stock-recrutement comprenne des courbes reproducteurs-recrues qui incluent la possibilité d'anticompensation et d'hypercompensation.

# Introduction

Many fish populations have declined drastically. Some stocks such as the Northern Atlantic cod (*Gadus morhua*) in eastern Canada (Hutchings and Myers 1994), sardines (*Sardinops sagax*) in California (Murphy 1966), and many whale species (Scarff 1977*a*, 1977*b*) have been fished below 1% of their original population sizes. Whether a severely reduced population can recover and if so, how quickly, depends on the population growth rate at low densities. The simplest population models, such as the logistic equation, predict higher rates of growth at lower abundances because of reduced intraspecific competition. This type of process has been called compensation, occurs when growth rates are reduced at low densities.

In problems of population viability analysis, models with depensation predict much higher probabilities of decline and extinction than do compensatory models. Understanding the

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role of depensation in the dynamics of fished stocks is essential in determining to what degree and how rapidly a population will recover when fishing effort is reduced. A number of mechanisms have been used to explain how depensation might occur. These include predator pits, reduced reproductive success, impaired aggregation, conditioning of the environment, efficiency of food location, and inbreeding (Hilborn and Walters 1992; Parkinson 1990; Emlen 1984; Asmussen 1979).

When a predator removes a relatively constant number of prey, the percentage of the prey population lost to predation increases as the population declines. This mechanism for depensation has been supported by a number of studies. Wood (1987) examined predation by the common merganser (Mergus merganser) on juvenile Pacific salmon during seaward migration in two streams where populations were enhanced by hatcheries and spawning channels. He found that maximum rates of salmon mortality due to merganser predation declined with increased salmon abundance (i.e., depensatory mortality). Using a statistical model, Crittenden (1994) found that incorporating depensatory mortality along with weak compensation during smolt migration explained a significant amount of the variation in adult returns. Peterman (1980) showed that several Native American subsistence fisheries in British Columbia behave like predators that become saturated. He used this result to explain the depensatory dynamics of the fished stocks suggested by data. However, Peterman and Gatto (1978) suggested that for many salmon stocks the natural predators are not being saturated.

Parkinson (1990) constructed a model of school formation for juvenile sockeye salmon (*Oncorhynchus nerka*). At lower population levels, increased predation rates are predicted because of longer school formation time and smaller schools. Montgomery et al. (1996) investigated the effects of spawning chum salmon (*Oncorhynchus keta*) on bed surface grain mobility in streams. They found that grain mobility was reduced decreasing the chances of streambed scour and therefore excavation of salmon embryos. They concluded that "Such a feedback between salmon spawning and bed mobility would make it increasingly difficult to reverse declining populations because decreased spawning activity would increase susceptibility to scour, leading to higher embryo mortality."

Myers et al. (1995) examined data sets from 129 fish stocks to look for evidence of depensation. They used a likelihood ratio test to compare the standard Beverton–Holt model with a modified Beverton–Holt model that allows for depensation. Of the 26 stocks for which the test had an estimated power over 0.95, only three resulted in the choice of the hypothesis with depensation while 11 rejected in the other direction (i.e., higher recruits per spawner at low densities than would be expected by the standard Beverton–Holt model). They conclude that the stock collapses observed up to now cannot be explained by depensation and "the effects of overfishing are, at this point, still generally reversible."

While these results are generally comforting to those involved in fisheries management, they do not provide much help in the management of individual stocks. If we accept the Myers et al. result that 3 of 26 stocks showed a statistically significant level of depensation, should a manager of another stock assume that there is a 3 in 26 chance of there being depensation in that stock? If so how much depensation? Myers et al. did not examine the effect of the intensity of depensation on the statistical significance. A manager would ideally like to know how probable different levels of depensation are for a particular type of fish. Presumably every stock within a certain group of fish (e.g., taxon) has a unique level of depensation, and we are interested in the distribution of these levels within that group.

One could fit the Myers et al. model to a group of stocks and then create a histogram from the resulting estimates of the depensation parameter. This assumes that the stocks used are representative of the larger group of interest (e.g., gadiforms, salmonids, etc.) There are two problems with this approach. The first is that a data set where the depensation parameter is very well estimated receives the same weight as one where the parameter is poorly estimated. Second, variability due to measurement error in the depensatory parameter is not differentiated from the variability between stocks in the depensatory parameter (the distribution we would like to know). By making no attempt to factor out variability associated with measurement error the estimated distribution is broader than necessary.

A second approach, used by McAllister et al. (1995) for another type of parameter, is to estimate the conditional probability distribution  $p(d_i|x_i)$  of a depensatory parameter *d* for each stock *i* (where  $x_i$  is the spawner–recruit data for stock *i*) and then average across the *n* stocks for which there are data:

(1) 
$$p(d) = \sum_{i=1}^{n} p(d_i | x_i) \frac{1}{n}$$

An advantage to this technique is that more information from each stock is being used (the likelihood function instead of just a point estimate). However, it still suffers the same problems as the first method. For example when there are a large number of uninformative data sets they dominate producing a very flat distribution in spite of many other informative stocks.

Regardless of how the distribution is estimated, for it to be useful, it is important that the measure of depensation used is easily interpretable. The depensatory parameter used by Myers et al. does not have a simple biological interpretation and is ambiguous when presented without the other parameters of the model.

Because most data sets provide little information about depensation (because of high variability and few observations at low spawner levels) it is normal practice not to consider depensation as a possibility. The purpose of this paper is to use the same data as Myers et al. to calculate a prior probability distribution for a depensation parameter that can be used in the analysis of other similar fish stocks. We accomplish this through the following steps.

(*i*) Introduce a spawner–recruit model that allows for depensation.

(*ii*) Reparameterize the model to include a more biologically interpretable depensatory parameter.

(*iii*) Estimate the marginal likelihood function of this depensatory parameter for each stock.

(*iv*) For each taxonomic group estimate the distribution of the depensatory parameter based on the likelihoods from step *iii*.

# **Materials and methods**

The Beverton–Holt spawner–recruit curve can be modified to allow for depensation by raising each occurrence of spawners (S) in the right-hand side of the equation to the power d:

(2) 
$$R = \frac{aS^d}{b^d + S^d}$$

For d = 1, the model displays the normal Beverton–Holt spawner– recruit relationship. A reduced rate of recruitment at low spawner levels, or depensation, occurs for d > 1. For d < 1, hypercompensation, recruitment is elevated at low densities. The parameter *a* is the asymptote that recruitment approaches as spawner levels become large and *b* is the level of spawners that produce a/2 recruits. In this parameterization, *d* is identical to the depensatory parameter,  $\delta$ , that Myers et al. (1995) used.

# A meaningful depensation parameter for the Beverton–Holt curve

The depensation parameter *d* has no straightforward biological interpretation and is not a particularly good measure of the intensity of depensation. A *d* value of 2.0 may indicate intense depensation or very slight depensation depending upon the other parameters of the model. To illustrate the problem we consider two *a,b,d* combinations  $(a_1,b_1,d_1 \text{ and } a_2,b_2,d_2)$ , where  $d_1 = d_2$ , yet the  $a_1,b_1,d_1$  triple shows a higher degree of depensation (Fig. 1). This is because the parameter *a* also has a large effect on the degree of depensation.

For this reason we reparameterize the model from a,b,d to  $\mathbb{R}^*,z,q$ , where q is the depensatory parameter and  $R^*$  and z are adapted from Mace and Doonan (1988). We begin by setting  $S^*$  equal to the maximum observed spawner level. The parameter  $R^*$  is then defined as the recruit level corresponding to  $S^*$  (Fig. 2):

(3) 
$$R^* = \frac{aS^{*d}}{b^d + S^{*d}}$$

**Fig. 1.** Two spawner–recruit curves with the same *d* illustrating the potential ambiguity of *d* as a measure of depensation.



and z is calculated as the proportion of  $R^*$  corresponding to the model at  $0.5S^*$ :

(4) 
$$z = \frac{\left(\frac{a(0.5S^*)^d}{b^d + (0.5S^*)^d}\right)}{R^*}$$

Next the parameters a' and b' are found for the standard Beverton– Holt curve that agrees with the depensatory model at  $0.5S^*$  and  $S^*$  (i.e., such that both curves have the same  $R^*$  and z):

(5) 
$$R = \frac{a'S}{b'+S}$$

Finally q is defined as the ratio of the depensatory and standard models at  $0.1S^*$ :

(6) 
$$q = \frac{\left(\frac{a(0.1S^*)^d}{b^d + (0.1S^*)^d}\right)}{\left(\frac{a'(0.1S^*)}{b' + (0.1S^*)}\right)}$$

This measure of depensation is less ambiguous, has a simple biological interpretation, and can be explained graphically (Fig. 2). For q < 1 the model is depensatory, while q > 1 results in hypercompensation. The parameters a' and b' are calculated by setting d = 1 and solving eqs. 3 and 4 simultaneously for a and b:

(7) 
$$a' = \frac{0.5R^*z}{z - 0.5}$$
  
(8)  $b' = \frac{0.5S^*(1 - z)}{z - 0.5}$ 

Because the Beverton–Holt model increases over its entire range, z falls between 0 and 1 (i.e., the model at  $0.5S^*$  will never be greater than the model at  $S^*$ ). Also, q is clearly bounded below by 0 and the upper bound is approximately 1.55 (Appendix 1).

#### Estimating the likelihood function of the depensatory parameter

Because we are interested in a distribution of q, independent of the other two parameters (z and  $R^*$ ) we would like to calculate the marginal likelihood of q, L(q | data) (or p(data | q)). However, integrating over z and  $R^*$  is computationally demanding and difficult to standardize for all of the stocks. For this reason we chose to estimate the marginal likelihood of q with the likelihood profile (Meeker and Escobar 1995; Venzon and Moolgavkar 1988). The likelihood profile is calculated by maximizing the full likelihood over z and  $R^*$ :

(9) 
$$\hat{L}(q|\text{data}) \approx \frac{\max}{R^*, z} L(q, z, R^*|\text{data})$$

We use the model:

(10) 
$$R = f(S)e^{t}$$

where *f* is the spawner–recruit relationship described above and *V* is a normal random variable with mean 0 and standard deviation  $\sigma$ . Because the mean of *V* is 0, *f*(*S*) is the median but not the mean of the log normally distributed random variable *R*. Instead of including  $\sigma$  as a free parameter we used the estimate from the model:

(11) 
$$\hat{\sigma}^2 = \frac{\sum_{i=1}^{n} (\ln(R_i) - \ln(f(S_i)))}{n-3}$$

Since there is no closed-form transform from  $R^*, z, q$  to a, b, d, the profiles were produced using an algorithm that systematically covers the a, b, d parameter space and transforms the results into the z, q parameter space (Appendix 2).

# Estimating the distribution of the depensatory parameter for a taxonomic group

Now that we have a likelihood function for each stock within a taxonomic group we would like to combine this information to produce a distribution describing the variability in the depensatory parameter, q, for that taxon. In the introduction we described two methods and pointed out that in both cases no effort is made to separate measurement error from the between stock variability in which we are interested.

In the approach we use, hierarchical modeling, the two sources of variability are explicitly included in the model so that the between stock distribution of the depensatory parameter can be more successfully isolated.

#### **Hierarchical modeling**

Hierarchical modeling is a Bayesian technique that can be used to combine data from several independent sources. Examples of applications include the analysis of toxoplasmosis rates in El Salvador cities (Efron and Morris 1975) and the prediction of freshman grade point averages based on data from a large group of law schools (Rubin 1980). Gelman et al. (1995) provide a good introduction to this technique. We describe hierarchical modeling in the context of our specific application.

The first step is to describe for each stock the uncertainty in the estimate of the depensatory parameter. This is characterized by the marginal likelihood of q,  $p(x_i|q_i)$ , where  $x_i$  is the data for the *i*th stock. We described the estimation of this function in the previous section. With hierarchical modeling we can also account for the betweenstock variability in q. This is done by allowing the  $q_i$ s (the depensatory parameter for each stock) to be random variables that follow a common distribution (Fig. 3). This distribution of the  $q_i$ s is what we would like to estimate. The parameter q has a lower and upper bound (0 to 1.55), but we are not sure what shape the distribution will take on. Because the beta distribution is bounded below and above and can take on a wide variety of symmetric and asymmetric shapes, it is a natural choice for describing variability in q. (Because the domain of the beta distribution is from 0 to 1 and q ranges from 0 to 1.55, we adopted a scaled q, q' = q/1.55, for the analysis. However, we will refer to q' as q to simplify the notation.):

(12) 
$$p(q_i | \alpha, \beta) = Beta(\alpha, \beta) = \frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} q_i^{\alpha - 1} (1 - q_i)^{\beta - 1}$$

Here  $\alpha$  and  $\beta$  are called hyperparameters because they are the parameters for a distribution of parameters.

By assuming that the stocks used in the analysis are a random sample from the stocks of interest we can calculate the joint distribution for all of the  $q_i$ s given  $\alpha$  and  $\beta$  as the product of the individual distributions:

**Fig. 2.** The graphical definition of  $R^*$ , *z*, and *q*, where q = n/m.



Fig. 3. In a fully Bayesian hierarchical model there are three levels of random variables: the hyperparameters  $\alpha$  and  $\beta$ , the parameters  $q_i$ s, and the data sets  $x_i$ s.



where  $q = (q_1, q_2, ..., q_n)$ . Similarly the joint likelihood of all of the stocks  $\tilde{c}$  an be written:

(14) 
$$p(\underline{x}|\underline{q}) = \prod_{i=1}^{n} p(x_i | q_i).$$

We can now use Bayes' theorem to combine these two components with a prior for the hyperparameters (the hyperprior; Appendix 3) to produce a joint posterior distribution for all of the parameters:

(15) 
$$p(\underline{q},\alpha,\beta|\underline{x}) \propto p(\underline{x}|\underline{q},\alpha,\beta) p(\underline{q},\alpha,\beta) = p(\underline{x}|\underline{q}) p(\underline{q}|\alpha,\beta)$$
  
  $\times p(\alpha,\beta)$ 

Note that, because the hyperparameters,  $\alpha$  and  $\beta$ , affect  $\underline{x}$ , the data, only through the parameters q, we have:  $p(\underline{x} | \underline{q}) = p(\underline{x} | \underline{q}, \alpha, \beta)$ . Also  $p(q, \alpha, \beta) = p(q | \alpha, \beta) p(\alpha, \beta)$ .

By integrating eq. 15 over the  $q_i$ s (Appendix 3) we get the marginal posterior probability distribution of the hyperparameters:

This describes the uncertainty about the shape of the distribution of 
$$q$$
's within the taxon given the data. Finally, multiplying this by the conditional distribution  $p(q | \alpha, \beta)$  and integrating over  $\alpha$  and  $\beta$  produces the distribution we are interested in:

(17) 
$$p(q) = \int_{\alpha} \int_{\beta} p(q | \alpha, \beta) p(\alpha, \beta) d\beta d\alpha$$

When analyzing data for a new stock from the same taxon p(q) can be used as an informative prior:

(18) 
$$p(q|x_{\text{new}}) \propto p(q)p(x_{\text{new}}|q)$$

where  $x_{\text{new}}$  is the data from the new stock.

#### The data

We use spawner–recruit data compiled by Myers et. al. (1995) from 114 stocks. The stocks include clupeiforms, gadiforms, pleuronectiforms, and salmoniforms and are located throughout the world. We chose to include only stocks with spawner–recruit time series of 15 or more years.



Fig. 4. Spawner-recruit data for four stocks with the best fit lines included and the corresponding likelihood profiles with beta fits (the lines).

# Results

# **Individual stocks**

The likelihoods for individual stocks convincingly mirror the uncertainty about depensation within a particular data set. For example, there were very few data at low spawner levels for many of the clupeiform and gadiform stocks, which tended to produce broad uninformative likelihoods. This can be seen in the Gulf of Finland herring stock, where there are no data at low spawning stocks and the resulting profile is very flat reflecting the absence of information about depensation (Fig. 4). In contrast, the northwestern Vancouver Island herring stock has a number of years at low spawner levels producing a more defined distribution. The Chilko Lake sockeye salmon population has an even higher percentage of years with low spawner levels yielding yet a narrower distribution. Because there are a



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number of low spawner years with relatively low recruit levels, a significant proportion of the probability falls in the range of depensation. In one of the three examples where Myers et al. (1995) rejected in favor of depensation, the Prince William Sound pink salmon data set results in a likelihood with most of its mass well to the left of q = 1. This is sensible given the disproportionately low recruit levels at low spawner populations and the low variability.

The beta approximations to the profiles (Appendix 3) fit relatively well. The sum of squares residual from the fit of the beta distribution to the profile for the northwestern Vancouver Island herring stock in Fig. 4 is 0.0033. The average sum of squares residual for the total 114 stocks is 0.0019.

#### The hierarchical model

For each of the four taxa the distributions for q, resulting from the hierarchical model, allowed for significant depensation. The salmonid distribution shows the least degree of variability with more than 95% of the probability between q = 0.5 and q = 1.4. The other three taxa, clupeiforms, gadiforms, and pleuronectiforms, have distributions with broad tails extending over the entire range of q. With the exception of the pleuronectiforms all the distributions had modes to the right of one (hypercompensation). In the case of the pleuronectiforms, the mode was between 0.8 and 0.9. For each of the four taxa the hierarchical modeling distributions were more narrow than those produced by histograms of the point estimates (Fig. 5).

The most difficult part of using hierarchical modeling on this problem was constructing an "uninformative" prior for  $\alpha$ and  $\beta$  (the hyperprior). The different priors we used resulted in different posteriors. This sensitivity to the hyperprior illustrates the degree of uncertainty about *q* in the data. A more informative data set would produce a posterior that is relatively robust to changes in the prior.

Uniform priors on  $\alpha$  and  $\beta$  and  $\ln(\alpha)$  and  $\ln(\beta)$  produced posteriors with a narrow band of high probability extending from low values of  $\alpha$  and  $\beta$  to infinite values of  $\alpha$  and  $\beta$ . This band is defined by the line  $m = (\alpha - 1)/(\alpha + \beta - 2)$  where *m* is the mode of the beta distribution with parameters  $\alpha$  and  $\beta$ . For small  $\alpha$ s and  $\beta$ s the variance is high, whereas large  $\alpha$ s and  $\beta$ s produce distributions with small variance. In the hierarchical model the large  $\alpha$ s and  $\beta$ s are possible by forcing all the *q*s to be very close to the mode *m*. The result is an improper posterior. A more sensible prior is the uniform distribution over the mean,  $\alpha/(\alpha + \beta)$ , and an approximation of the standard deviation,  $1/(\alpha + \beta)^{1/2}$  (Gelman et al. 1995). These parameters are more readily interpreted and are bounded above and below when  $(\alpha + \beta)$  is constrained to be greater than a positive constant (we chose 1).

### Discussion

By creating distributions for a depensatory parameter, we found that there is a significant amount of uncertainty about whether depensation exists and to what degree. Although, as Myers et al. (1995) showed, hypothesis tests do not provide convincing evidence for widespread depensation, the fact that broad tails in the distributions for each of the four taxa extend well into the depensatory range suggests that not allowing for the possibility of depensation in fish population dynamics is a poor assumption, given these data.

The results presented here can be used directly as prior distributions for q in a Bayesian stock assessment. This is done by first fitting a population dynamics model to data from a stock of interest to create the joint likelihood function for the model parameters. The posterior distribution for these parameters can then be calculated using a prior (constructed in part with the q distribution) and Bayes' theorem. This can be used to calculate the probability of different states of nature, which in turn can be used in a decision analysis to calculate expected biological and economic outcomes. By using an informative prior in this process, depensation is allowed for without claiming complete ignorance. For an example of this type of analysis see McAllister et al. (1994). The usefulness of these distributions is not restricted to Bayesian analysis. They can also be included as a likelihood component in a maximum likelihood analysis.

The analysis of Myers et al. illustrates the general incompatibility between tests of hypotheses and decision making. Bayesian methods provide a result that can be directly incorporated into decision making. Traditional hypothesis testing, by not distinguishing between statistical and biological significance and by not providing any indication of the relative likelihood of competing hypotheses, serves little purpose for fishery managers.

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# **Appendix 1.** The boundary of the *z*,*q* parameter space.

The *z*,*q* parameter space, or range of possible *z*,*q* combinations, can be calculated by solving for *q* in terms of *z*. The parameter *q* is defined as

(1-1) 
$$q = \frac{\left(\frac{a(0.1S^*)^d}{b^d + (0.1S^*)^d}\right)}{\left(\frac{a'(0.1S^*)}{b' + 0.1S^*}\right)}$$

From eqs. 7 and 8 we have a' and b' in terms of z and  $R^*$ . We do the same for a and b resulting in

(1-2) 
$$a = \frac{R^*(1-0.5^d)z}{z-0.5^d}$$

(1-3) 
$$b = \left(\frac{(0.53^{-1})^2(1-z)}{z-0.5^d}\right)^{ad}$$

Substituting eqs. 7, 8, 1-2, and 1-3 into 1-1 and simplifying gives

(1-4) 
$$q = \frac{(1-0.5^d) \left[ \frac{0.5}{0.1} (1-z) + (z-0.5) \right]}{(1-0.5) \left[ \frac{0.5^d}{0.1^d} (1-z) + (z-0.5^d) \right]}$$

Now we translate the constraints on the original parameters *a*, *b*, and *d* to constraints on *q* and *z*. First we have b > 0. Now from eq. 1-3 we can see that b > 0 as long as  $0.5^d < z < 1$ . Second, we have the constraint a > 0. From eq. 1-2 this will be true if  $z > 0.5^d$ . So on the boundary,  $z = 0.5^d$ . Solving for *d*, we can substitute  $\ln(z)/\ln(0.5)$  for all the *d*s in eq. 1-4. This gives us a function for *q* in terms of only *z*:

(1-5) 
$$q = \frac{0.1^{\frac{\ln(z)}{\ln(0.5)}} \left[ \frac{0.5}{0.1} (1-z) + (z-0.5) \right]}{(1-0.5)z}$$

**Fig. A1.** Boundaries in the *z*,*q* parameter space correspond to boundaries in the *a*,*b*,*d* parameter space. The curves for a = 0 and d = 0 are defined by eqs. 1-5 and 1-6, respectively.



Finally, we look at the constraint d > 0. Setting d = 0 in eq. 1-4 results in 0/0. To find the limit for eq. 1-4 as d approaches 0, we use l'Hospital's rule to arrive at

(1-6) 
$$q = \frac{-\ln(0.5)\left[\frac{0.5}{0.1}(1-z) + (z-0.5)\right]}{(1-0.5)\left[\ln\left(\frac{0.5}{0.1}\right)(1-z) - \ln(0.5)\right]}$$

Plotting the three constraints in *z*, *q* space shows that b > 0 and a > 0 define the *z*, *q* parameter space (Fig. A1). The largest possible *q* can be found by setting the first derivative of eq. 1-5 equal to 0, solving for *z*, and evaluating eq. 1-5 at the resulting *z*. This produces q(z = 0.786 34) = 1.550 49.

#### **Appendix 2.** Computing the likelihood profiles.

Because the model we are using has only three parameters, it is feasible to characterize the likelihood surface by evaluating it at points on a three-dimensional grid. Because there is no closed-form inverse function for the transform from a,b,dspace to  $R^*, z, q$  space, we searched over a,b,d and recorded the maximum likelihood for the a,b,d triples that fell in each cell of a z,q table.

Because we were dealing with a large number of data sets with varying parameter ranges, it was not feasible to iterate over a prespecified volume. Instead, the algorithm started at

# **Appendix 3.** The hierarchical modeling details.

# Integrating over the $q_i$ s

Integrating over all the  $q_i$ s numerically would be computationally prohibitive because there are groups with over 30 stocks (i.e., 30 variables over which to integrate). We sidestep this problem by scaling each likelihood profile so that it integrates to one and then fitting a beta distribution to it using least squares. In this way we replace each data set  $x_i$  with the parameters of a beta distribution  $(u_i, v_i)$ :

(3-1) 
$$p(x_i|q_i) \approx p(u_i, v_i|q_i) = \frac{\Gamma(u_i + v_i)}{\Gamma(u_i)\Gamma(v_i)} q_i^{u_i - 1} (1 - q_i)^{v_i - 1}$$

The joint posterior probability distribution of the parameters and hyperparameters becomes

$$p(\underline{q}, \alpha, \beta | \underline{u}, \underline{v}) = \prod_{i=1}^{n} p(q_i | \alpha, \beta)$$

$$\times \prod_{i=1}^{n} p(u_i, v_i | q_i) p(\alpha, \beta)$$

$$\approx \prod_{i=1}^{n} \left( \frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} q_i^{\alpha - 1} (1 - q_i)^{\beta - 1} \right)$$

$$\times \prod_{i=1}^{n} \left( \frac{\Gamma(u_i + v_i)}{\Gamma(u_i)\Gamma(v_i)} q_i^{u_i - 1} (1 - q_i)^{v_i - 1} \right)$$

$$\times p(\alpha, \beta)$$

the maximum-likelihood estimate and moved away until the likelihood became negligibly small. This necessitates updating the maximums of the parameters in the inner loops as the outer loop parameters change.

By plotting the original parameters (a, b, d) against the new parameters  $(R^*, z, q)$  it became apparent that the mapping involved logarithmiclike relationships. For this reason using additive steps in the original parameter space led to increasingly large (or small) steps in the transformed space. This problem was reduced significantly by changing to multiplicative steps.

This simplifies to

(3-3) 
$$\frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)}\prod_{i=1}^{n} \left(\frac{\Gamma(u_{i}+v_{i})}{\Gamma(u_{i})\Gamma(v_{i})}q_{i}^{u_{i}+\alpha-2}(1-q_{i})^{v_{i}+\beta-2}\right) \times p(\alpha,\beta)$$

Using the fact that all distributions integrate to one, the integral over all *q*s can be calculated analytically to produce the marginal posterior probability distribution for the hyperparameters:

(3-4) 
$$p(\alpha, \beta|\underline{x}) \propto \prod_{i=1}^{n} \left( \frac{\Gamma(\alpha + \beta)\Gamma(\alpha + u_i - 1)\Gamma(\beta + v_i - 1)}{\Gamma(\alpha)\Gamma(\beta)\Gamma(\alpha + u_i + \beta + v_i - 2)} \right) \times p(\alpha, \beta)$$

### **Choosing a hyperprior**

Choosing a prior for  $\alpha$  and  $\beta$  in eq. 20 is not trivial. A uniform prior on  $\alpha$  and  $\beta$  results in an improper posterior. This is because very large values of  $\alpha$  and  $\beta$  yield a beta distribution with a very small variance. If all the *q*s are set to the same value, *m*, there are highly probable combinations of  $\alpha$  and  $\beta$  (i.e., all  $\alpha$ and  $\beta$  such that the mode  $(\alpha - 1)/(\alpha + \beta - 2)$  equals *m*) extending to infinity. A sensible alternative is to use a uniform prior on the mean,  $\alpha/(\alpha + \beta)$ , and a measure of variability  $1/(\alpha + \beta)^{1/2}$  (Gelman et al. 1995, p. 131) In the original parameters,  $\alpha$  and  $\beta$ , this translates to the distribution:

(3-5) 
$$p(\alpha, \beta) \propto (\alpha + \beta)^{-5/2}$$

Applying this hyperprior produces a proper posterior.