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A Meta-Analysis of the Habitat Carrying Capacity and Maximum Reproductive Rate of Anadromous Alewife in Eastern North America

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Abstract.—We analyzed the dynamics of eight populations of anadromous alewife *Alosa pseudoharengus* to determine their habitat carrying capacity, their maximum reproductive rate, and whether depensation occurs at low abundances. When spawner–recruit models are fit to data sets for individual alewife populations, the resulting parameter estimates are often poorly determined, biologically unrealistic, and highly variable among populations. When the spawner and recruit time series for all populations are standardized to the same scale, populations that are outliers and appear to be at low levels are immediately evident. We also used nonlinear mixed-effects models to estimate spawner–recruit parameters for the eight populations simultaneously. By assuming that the maximum reproductive rate and carrying capacity per unit area are random variables drawn from probability distributions that are characteristic of the species, among-population variability is greatly reduced, and the parameter estimates resulting from the mixed-effects model are biologically reasonable. While the maximum reproductive rate, which can be interpreted as the biological limit for anthropogenic mortality, shows little variability among populations, the carrying capacity per unit area varies by more than an order of magnitude among populations of this species. We did not find evidence of depensation in the eight populations examined.

Introduction

Spawner–recruit models are a widely accepted tool for analyzing population dynamics (Moussalli and Hilborn 1986; Myers et al. 1999), providing biological reference points for management (Myers et al. 1994; Myers and Mertz 1998a) and a framework for the estimation of the long-term consequences of mortality caused by pollution, dams, or other human activities (Barnthouse et al. 1988; Hayes et al. 1996). In this paper, we provide a detailed analysis of the population dynamics of anadromous alewife *Alosa psuedoharengus* using a two-parameter spawner–recruit model. One of these parameters, the maximum reproductive rate at low population size, is fundamental for determining the intrinsic growth rate, r_{max} (Cole 1954), for population viability analyses (Lande et al. 1997) and calculation of many biological reference points for management (Mace 1994). The maximum reproductive rate is also the biological limit to overfishing and other sources of anthropogenic mortality (Crecco and Gibson 1990; Myers and Mertz 1998b). The other parameter, the habitat carrying capacity, is needed to determine the potential long-term yield for a fishery, the target spawning escapement for management (Moussalli and Hilborn 1986), and the size of fish passage facilities (Clay 1995) and can be used to compare habitat quality (Hayes et al. 1996). Together, the two parameters provide a basis for evaluating the status of a population and assessing the changes to the population resulting from habitat alterations or other human activities.

Traditionally, fisheries biologists have relied upon data only from the population of interest to assess the effects of pollution, fishing, and other activities. Unfortunately, the long and detailed time series that are required to arrive at firm conclusions simply do not exist for the majority of fish populations (Myers and Mertz 1998a). However,

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many populations of the same species (or closely related species) share similar life history strategies. For this reason, parameter estimates from several populations can be combined, providing a probability distribution for the parameter estimates at some higher organizational level such as the species (Myers et al. 1999, 2001). The resulting probability distributions can be combined with comparatively limited population-specific data to make inferences at the level of the specific population. In this way, the uncertainty of biological parameters used in fisheries management is reduced (Myers and Mertz 1998b). This approach, known as meta-analysis, allows conclusions to be reached by drawing upon data from many populations.

We therefore approached our analysis of alewife population dynamics in two ways: (1) we modeled the data sets for each population individually and (2) we used meta-analytic methods to estimate model parameters for the eight populations simultaneously. In so doing, we were able to determine how well spawner–recruit parameters are determined for individual populations and were also able to provide estimates of the reproductive rate and habitat carrying capacity for alewife at the species level.

We primarily used compensatory spawner–recruit models for our analysis. Implicit in their use is the assumption that per capita survival from the egg to the age of recruitment is a decreasing monotonic function of the number of eggs and that the maximum reproductive rate occurs at the origin. If there exists a spawner abundance threshold below which survival is an increasing function of the number of eggs, these models would overestimate the limits of exploitation. We therefore also examined our data for evidence of this phenomenon, which is known as depensation (Clark 1976; Myers et al. 1995).

Methods

We adapted the methods of Myers et al. (2001) and Barrowman (2000) for this meta-analysis. As discussed below, we began by standardizing our data so that estimates of spawner–recruit parameters among populations are comparable. After standardizing the data, we fit spawner–recruit models to the data for each population individually and assessed how well the parameter estimates were determined for each population. We then fit the models to all data sets simultaneously using a mixed-effects model. This model provided parameter estimates for each population that is weighted by the information contained in the data for other populations and a probability distribution for the parameter estimates for alewife at the species level.

The Data

We used spawner–recruit time series for eight alewife populations in eastern North America (Table 1). A statistical, age-structured, life history model designed specifically for *Alosa* spp. (Gibson and Myers 2003, this volume) was used to construct the spawner–recruit time series for four of these populations. This model was adapted to the data available for each population (catch at age and previous spawning data for each population, larval indices for the Margaree River population, and escapement counts for the Mactaquac Headpond and Gaspereau River populations). Existing spawner–recruit series were used for the other four populations.

Table 1.—Spawner–recruit time series used for the mixed effects modeling.

River	Spawning area (km^2)	Time series	Data source
Annaquatucket River, Rhode Island	1.0	1945–1989	Crecco and Gibson (1990)
Long Pond, Maine	3.9	1950–1955	Havey (1961)
Damariscotta River, Maine	18.1	1977–1984	Crecco and Gibson (1990)
Lamprey River, New Hampshire	0.2	1972–1985	Crecco and Gibson (1990)
Saint John River, New Brunswick	87.3	1968–1995	Life history model
Margaree River, Nova Scotia	57.4	1983–1995	Life history model
Miramichi River, New Brunswick	75.0	1982–1995	Life history model
Gaspereau River, Nova Scotia	22.9	1981–1995	Life history model

The Modeling Framework

Some assumptions about population regulation in alewife are necessary for the following analyses. We assumed that year-class strength of anadromous alewives is regulated primarily through intra-specific competition occurring during the premigratory larval and juvenile life stages. As such, the carrying capacity of freshwater nursery habitat is the factor that ultimately limits the size of an alewife population. This assumption is consistent with the critical period hypothesis and the concentration hypothesis (Beverton 1995) that implies that density-dependent processes should be greatest during life stages that are most concentrated in space (Hjort 1914). It is also consistent with population regulation in other *Alosa* species such as American shad *A. sapidissima* (Crecco and Savoy 1987). The carrying capacity of the nursery habitat may fluctuate from year to year about its median as environmental conditions within the nursery areas vary, contributing to the variability of the spawner–recruit relationship. While it is the carrying capacity of the nursery habitat that ultimately limits the size of an alewife stock, we express the carrying capacity as the size of the spawning run that would result in the absence of anthropogenic mortality. This makes our results directly comparable with stock assessments that provide estimates of the size of the spawning run for populations that are exploited or impacted by other human activities. Additionally, the majority of the available data are from the adult portion of the population.

We modeled the population dynamics of alewives using two equations, a spawner–recruit relationship that expresses recruitment as a density-dependent function of spawner biomass, and the replacement line, the slope of which is the inverse of the rate at which recruits produce replacement spawners. Here, an implicit assumption is that all density-dependent processes occur between spawning and recruitment. Therefore, we chose the age of recruitment to be age 3 (the earliest age of maturity for most stocks and the latest age that could reasonably be chosen) and defined recruitment for year-class t (R_t) as

$$R_t = \sum_{a=3}^{6} \left(\frac{N_{t+a,a}}{e^{-M_{\text{juv}}(a-3)}} \right) .$$

Here, $N_{t+a,a}$ is the number of fish of age a, in year $t + a$, that are returning to the river to spawn for the first time and M_{juv} is the instantaneous natural mortality rate of immature alewife while at sea. We assumed $M_{\text{juv}} = 0.4$ for all populations in our analysis based on the empirical relationship between natural mortality and longevity (maximum age of 11 years) derived by Hoenig (1983).

The Spawner–Recruit Relationship

The Beverton–Holt and Ricker models are the most commonly used two-parameter spawner–recruit models (Hilborn and Walters 1992). These models differ fundamentally in their assumptions of the underlying biology, the latter showing a decline in recruitment at higher spawner abundance, a phenomenon known as overcompensation. While this does not appear to be a characteristic of alewife populations (see Figure 1), we used a formal model selection criterion, the Akaike information criterion (Quinn and Deriso 1999), to choose between these models. The Beverton–Holt model provided the better fit for seven of the eight populations, and the fits were not significantly different for the eighth population. We therefore choose a Beverton–Holt spawner–recruit function for the remaining analysis and modeled the relationship between the spawning biomass in year t (S_t) and R_t as

$$R_t = \frac{\alpha S_t}{1 + (\alpha S_t / R_0)}.$$

Here, α is the slope at the origin of the spawner–recruit relationship and R_0 is the asymptotic recruitment level, which is the carrying capacity expressed as the number of fish that survive to age 3.

The Recruit–Spawner Relationship

We model the rate at which recruits produce spawners (the inverse of the replacement line) using a spawning biomass per recruit ($\text{SPR}_{F=0}$) calculation (Mace 1994) that we have adapted for alewife life history:

$$\text{SPR}_{F=0} = \sum_{a_{\text{rec}}}^{a_{\max}} \text{SS}_a w_a ,$$

where SS_a is given by

$$\begin{aligned}
\text{SS}_3 &= p_3 \\
\text{SS}_4 &= \text{SS}_3 e^{-M_{\text{ad}}} + (1-p_3)e^{-M_{\text{juv}}} p_4 \\
\text{SS}_5 &= \text{SS}_4 e^{-M_{\text{ad}}} + (1-p_3)(1-p_4)e^{-2M_{\text{juv}}} p_5 \\
\text{SS}_6 &= \text{SS}_5 e^{-M_{\text{ad}}} + (1-p_3)(1-p_4)(1-p_5)e^{-3M_{\text{juv}}} p_6 \\
&. \\
&.
\end{aligned}$$

$$SS_{a_{\max}} = SS_{(a_{\max}-1)}e^{-M_{ad}} + (1-p_3)(1-p_4)\ldots (1-p_{a_{\max}-1})e^{-(a_{\max}-3)M_{juv}}p_{a_{\max}}.$$

Here, a is the age of the fish, M_{juv} and M_{ad} are the instantaneous mortality rates for immature and mature fish, p_a is the probability that an immature fish that is alive at age a will mature at that age, and w_a is the age-specific weight. Note that this model can be used to calculate SPR-based reference points (Mace and Sissenwine 1993) by changing the mortality rates to include fishing mortality.

Values used in our calculation of $SPR_{F=0}$ are shown in Table 2 and are calculated from the life history model output for the Margaree River, Miramichi River, Gaspereau River, and Mactaquac Headpond. We used the mean of the Gaspereau River and Mactaquac Headpond $SPR_{F=0}$ values for the other four stocks on the basis of geographic proximity.

Data Standardizations

The eight spawner–recruit time series are not directly comparable for two reasons. First, the sizes of the spawning and nursery areas, and hence the quantity of habitat, differ among the eight popula-

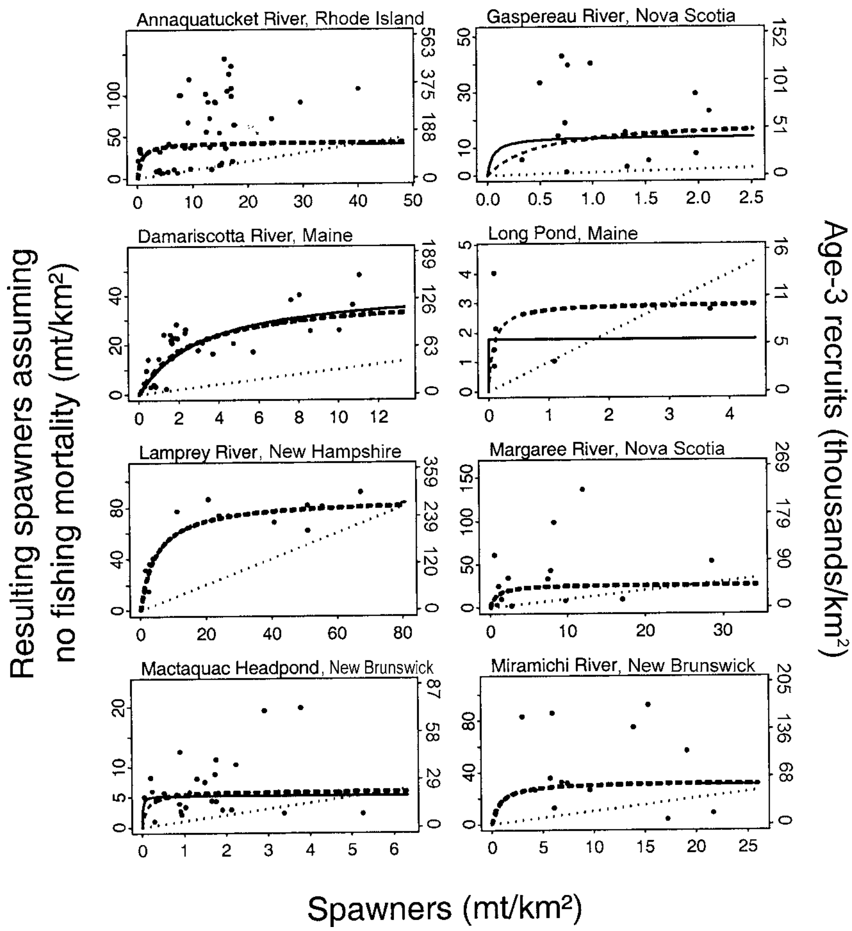

Figure 1.—Spawner–recruit relationships for eight alewife populations plotted on different scales to show the variability around the fitted models for each population. The scale on the right is the number of age-3 recruits produced in each cohort. The scale on the left shows the number of subsequent spawners that would be produced by these recruits in the absence of anthropogenic mortality. The solid line is the spawner–recruit relationship obtained for each population individually, the thick dashed line is the spawner–recruit relationship for each stock from the mixed-effects model, and the dotted line is the replacement line. The median carrying capacity occurs where the replacement line intersects with the spawner–recruit relationship. mt = metric tons.

Table 2.—Values used for calculation of spawning biomass per recruit ($\mathrm{SPR}_{F=0}$). The weights at age are taken from the Margaree River population. Maturity probabilities (p_a) are calculated from the life history model output for the Margaree River, Gaspereau River, Miramichi River, and Mactaquac Headpond. M is the instantaneous natural mortality rate.

Age		p_a					
(year)	Weight (g)	Margaree	Miramichi	Mactaquac	Gaspereau	M_{juv}	M_{adult}
3	213	0.51	0.37	0.07	0.05	0.4	1.0
4	267	0.97	0.91	0.45	0.60	0.4	1.0
5	312	0.81	0.82	0.76	0.95	0.4	1.0
6	351	1	1	1	1	0.4	1.0
7	394	1	1	1	1	-	1.0
8	415	1	1	1	1	-	1.0
9+	441	1	1	1	1	-	1.0

tions. We therefore standardized both the spawner and recruit time series for each population by dividing by the amount of the nursery habitat in each watershed. This standardization allows the productivity of different populations to be compared on a per unit area basis. Second, the rate at which recruits produce spawners differs among populations which implies that the size of the spawning run that would result from identical numbers of age-3 recruits also differs among populations. A second standardization corrects for this problem. We defined $\tilde{R}_t$ as the spawner biomass per unit area of nursery habitat that is produced by members of year-class t throughout their lives in the absence of anthropogenic mortality calculated as

$$\tilde{R}_t = R_t \cdot \mathrm{SPR}_{F=0}.$$

After this standardization, the slope of the replacement line equals one for all populations, all differences in the population dynamics are in the spawner–recruit portion of the model, and data and parameter estimates are directly comparable among populations.

In the spawner–recruit model, we denote our standardized parameters as $\tilde{\alpha}$ and $\tilde{R}_0$; $\tilde{\alpha}$ is now the maximum lifetime reproductive rate (Myers et al. 1999) and is the number of offspring (that survive to subsequently spawn) produced by a fish throughout its lifetime at low population sizes in the absence of anthropogenic mortality. As such, it is the biological limit for fishing and other sources of anthropogenic mortality. $\tilde{R}_0$ is the carrying capacity (the spawning run size in the absence of anthropogenic mortality) per unit area of nursery habitat.

The Statistical Models

We used the above framework to set up our statistical model. Assume we have several alewife populations, and for each population i, we have n_i observations of the form $(S_{ij}, \tilde{R}_{ij}), j = 1 \ldots n_i$. These observations are modeled as

$$\tilde{R}_{ij} = \frac{\tilde{\alpha}_i S_{ij}}{1 + \tilde{\alpha}_i S_{ij} / \tilde{R}_{0i}} e^{\varepsilon_{ij}},$$

where $\tilde{\alpha}_i > 0$, $\tilde{R}_{0i} > 0$, and $\varepsilon_{ij} \sim N(0, \sigma_i^2)$. As specified, error variance differs among populations, and errors are multiplicative. Taking the natural logarithms of both sides yields:

$$\log_e \tilde{R}_{ij} = \log_e(\tilde{\alpha}_i) + \log_e(S_{ij}) - \log_e\left(1 + \frac{\tilde{\alpha}_i S_{ij}}{\tilde{R}_{0i}}\right) + \varepsilon_{ij}.$$

We define $\log_e(\tilde{\alpha}_i) = a + b_i$ and $\log_e \tilde{R}_{0i} = c + d_i$:

$$\log_e \tilde{R}_{ij} = a + b_i + \log_e(S_{ij}) - \log_e\left[1 + \left(\frac{\exp(a + b_i) S_{ij}}{\exp(c + d_i)}\right) + \varepsilon_{ij}\right].$$

We fit this model under two assumptions about a, b_i, c, and d_i. First we treat a, b_i, c, and d_i as fixed effects. This is the equivalent to fitting to each spawner–recruit series individually and does not take advantage of similarities between model parameters among populations of a taxonomic group. The second method takes advantage of these similarities. We assumed that $\log_e \tilde{\alpha}_i$ and $\log_e \tilde{R}_{0i}$ are normally distributed random variables and fit the model treating a and c as fixed and b_i and d_i as random effects. Here, a and c are the means of $\log_e \tilde{\alpha}_i$ and $\log_e \tilde{R}_{0i}$ respectively, and b_i and d_i are the random deviates for each population, such that

$$\begin{pmatrix} b_i \\ d_i \end{pmatrix} \overset{iid}{\sim} N\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_b^2 & 0 \\ 0 & \sigma_d^2 \end{pmatrix}\right].$$

Note that when estimated using this model, $\tilde{\alpha}_i$ and $\tilde{R}_{0i}$ are the median maximum lifetime reproductive rates and median carrying capacities.

We used a sigmoidal Beverton–Holt model (Thompson 1993) to look for evidence of depensation:

$$\tilde{R}_{ij} = \frac{\tilde{\alpha}_i S_{ij}^{\delta_i}}{1 + \tilde{\alpha}_i S_{ij}^{\delta_i} / \tilde{R}_{0i}} e^{\varepsilon_{ij}}.$$

Here, a value of $\delta > 1$ gives a depensatory model, $\delta = 1$ is the original Beverton–Holt model, and $\delta < 1$ is a model with a sharper bend than the Beverton–Holt. We fit this model to the data for each stock individually and to all stocks simultaneously using a mixed-effects model as above.

The mixed-effects model is an alternative to the hierarchical Bayes approach (Carlin and Louis 1996) that does not require the specification of a joint prior distribution for the fixed effects and variance components. Estimates are obtained using maximum likelihood and are identical to empirical Bayes estimates (often referred to as MLE priors) in that the priors are obtained from the data. As such, they can be used as priors for Bayesian analyses of population dynamics for stocks where little data exists about the stock under investigation (Myers et al. 2002). Here, we obtain estimates for our models using the approximate maximum likelihood algorithm of Lindstrom and Bates (1990) and the S-Plus nonlinear mixed-effects library of Pinheiro and Bates (1999).

Results

Figures 1 and 2 show two views of the data and fitted models for each population. The Lamprey River, New Hampshire, data show little scatter around the fitted models (Figure 1), although the other populations show considerable variability about the model. For populations such as the Miramichi River, Mactaquac Headpond, and Long Pond, Maine, the slope at the origin for the individual models is unrealistically very steep , suggesting almost no relationship between spawner abundance and recruitment (Figure 1). The mixed-effects model provides much lower slopes at the origin for these populations. Figure 2 is similar to Figure 1, but shows the data for each population on the same scale. For the five populations where the maximum observed spawner abundance exceeds 10 metric tons/km^2, the patterns are very similar, and the carrying capacity ranges from 27 to 86 metric tons/km^2. Two of the other populations, the Mactaquac Headpond and Long Pond, are distinctly dissimilar from the other populations, and their maximum observed spawner abundance is very low in comparison with the other populations. These populations resulted by providing access to impoundments. The data for Long Pond was collected during the first few years of re-colonization, and escapement is controlled at the Mactaquac Headpond. The eighth population, the Gaspereau River, is impacted by fishing and hydro-electric development, and spawner abundances are low relative not only to the other populations, but also to the estimated carrying capacity for that watershed.

Figure 3 is a meta-analytic summary of the individual fits for each population and the mixed-effects model results for alewife at the species level. The raindrop plots (Barrowman 2000) for each population (light gray shaded region) show the profile likelihood for each parameter, the width of which can be used to gauge the relative plausibility of different values. When estimated for each stock individually, the maximum lifetime reproductive rate was well determined for only two of the eight populations. The lower bounds of the confidence intervals are determined for the other populations, but no upper limit can be determined from the data, as shown by the ramped profiles. For the Long Pond and Miramichi River populations, the estimates of the maximum lifetime reproductive rates are essentially infinite. For stocks where the likelihoods are not approximately normal, the conventional, symmetrical 95% confidence intervals are not adequate approximations of the uncertainty of the estimates. The mixed model output shows that at low abundance, in the absence of intra-specific competition, alewives produce about 34.1 replacement spawners throughout their lives. The mixed model random effects distribution for $\log_e \tilde{\alpha}$ has a mean of 3.53 and a standard deviation of 0.72.

Overall, the individual data sets contained more information about the habitat carrying capacity than the maximum lifetime reproductive rate, although carrying capacities varied widely among populations (Figure 3). The median habitat carrying capacity for alewife populations in terms of the biomass of fish in the spawning run is 21.3 metric tons/km^2, or assuming a mean weight of 0.23 kg/fish, about 92,000 fish. The mixed model random effects distribution for $\log_e \tilde{R}_0$ has a mean of 3.06 and a standard deviation of 1.07.

The estimates of the maximum lifetime reproductive rate for the individual stocks resulting from the mixed-effects model showed considerably less variability than those from the individual fits (Figure 4). Because the habitat carrying capacities were better determined by the individual fits than the maximum reproductive rate, their variability showed less "shrinkage" when estimated with the

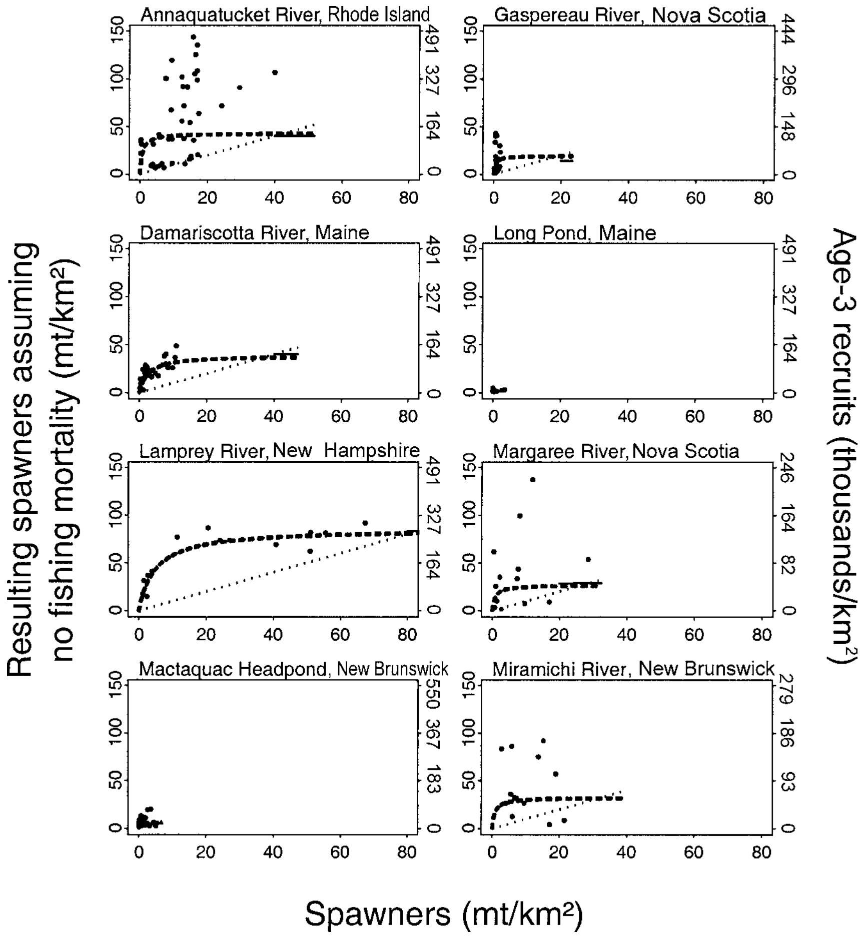

Figure 2.—Spawner–recruit relationships for eight alewife populations plotted on the same scale to show the variability among populations. Line symbolism is identical to Figure 1. mt = metric tons.

mixed model than did the variability for maximum reproductive rates (Figure 4). Median habitat carrying capacity ranged from a low of 3.0 metric tons/km^2 for the Long Pond population to 86.1 metric tons/km^2 for Lamprey River.

We did not find evidence of depensation in these data sets at the observed levels of abundance. Five of the eight data sets contained little or no information about depensation (Figure 5), and for two of the remaining data sets, the depensation parameter was very close to one. The mixed-effects model median (0.66) is not significantly different from one (Figure 5).

Discussion

Our analysis of the population dynamics of anadromous alewife has uncovered a number of interesting factors about the biology of this species and shows how information about individual populations can be evaluated using meta-analysis. Even if one ignores the modeling, when the data for several populations are simply standardized and plotted on the same scale (Figure 2), patterns become evident, and populations that are different are easily identified. For example, looking only at the plot for the Mactaquac Headpond in Figure 1, the plot is similar to many other spawner–recruit plots for other populations and species; there is scatter around the fitted spawner–recruit relationship and what appears to be a reasonable range of spawner abundances relative to the predicted equilibrium abundance. Parameter estimates can be obtained for this stock based on an individual fit, which exemplifies the traditional approach to spawner–recruit modeling. However, when the data are stan-

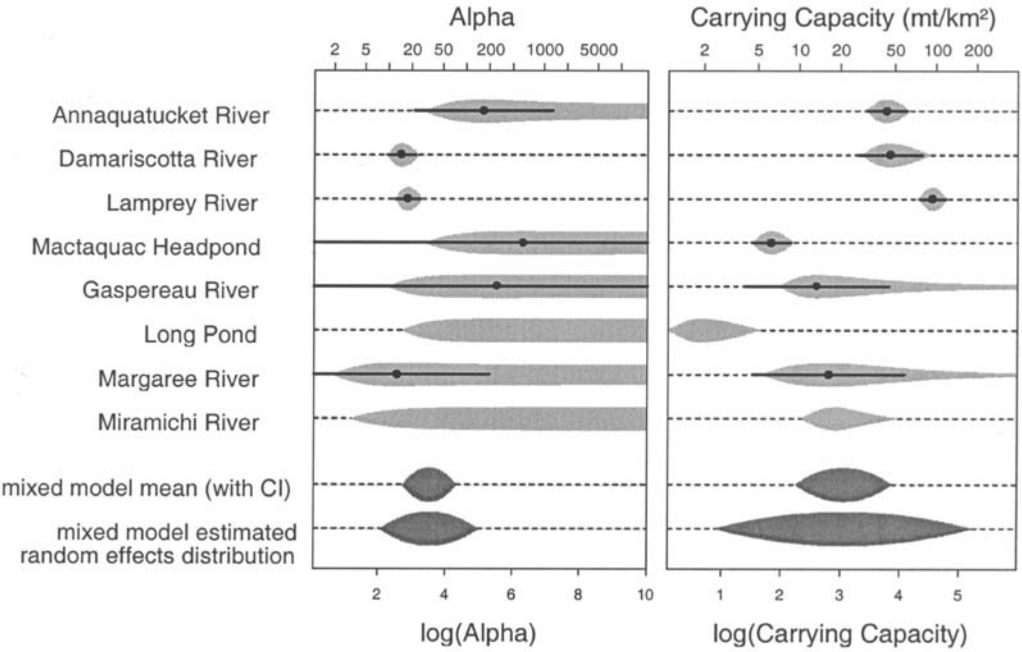

Figure 3.—A meta-analytic summary of the maximum lifetime reproductive rate (alpha) and the habitat carrying capacity (metric tons/km^2) for eight alewife populations. The light gray shaded regions are individual fits that depict the profile likelihood for each parameter, truncated to show the 95% confidence intervals (CI). The height of the profile is used to gauge the relative plausibility of different values (greater height is more plausible). The black dots are the maximum likelihood estimates for each parameter. Convergence of the nonlinear least-squares algorithm was not obtained for the Miramichi and Long Pond stocks. Where convergence was obtained, approximate asymptotic 95% CI are shown (black lines). The dark gray shaded regions show summaries of the mixed model results. The mixed model mean represents the estimated mean of the logarithm of each parameter with a 95% CI. The mixed model estimated random effects distribution is the normal distribution for the logarithm of each parameter based on its mean and variance estimated with the mixed-effects model.

dardized and plotted in a way that they can be compared to other populations (Figure 2), it is immediately apparent that either this population, or its data, is different from the five populations where the range of observed spawner abundances is larger. For populations such as the Mactaquac Headpond, where the spawner abundance is low relative to the other populations, carrying capacity is probably being underestimated. This is not evident from an individual graph such as that shown in Figure 1. For these populations, spawner abundance would need to be increased to confirm whether the range of data is insufficient to accurately estimate spawner–recruit parameters or whether the population is indeed different from other alewife populations. The experimental manipulation of spawner abundance to meet data requirements for management has been strongly advocated (Walters 1986), and artificial reservoirs where spawner escapement is already controlled provide the ideal location for this kind of experimentation. However, this active approach to fisheries management has proven difficult to implement in practice (Jessop 1990).

One of the most interesting factors to come out of our analysis is the relative constancy of the maximum lifetime reproductive rate of alewife among populations. When analyzed individually, the maximum lifetime reproductive rate was well determined for only two of the eight populations. The maximum likelihood estimates for the other six populations were highly variable, had wide confidence intervals, and, for the Long Pond and Miramichi River populations, were biologically unrealistic. When estimated using the mixed-effects model, the variability among populations was greatly reduced, and realistic estimates were obtained for all populations.

Our estimate of the maximum lifetime reproductive rate for alewife (31.4) is high relative to

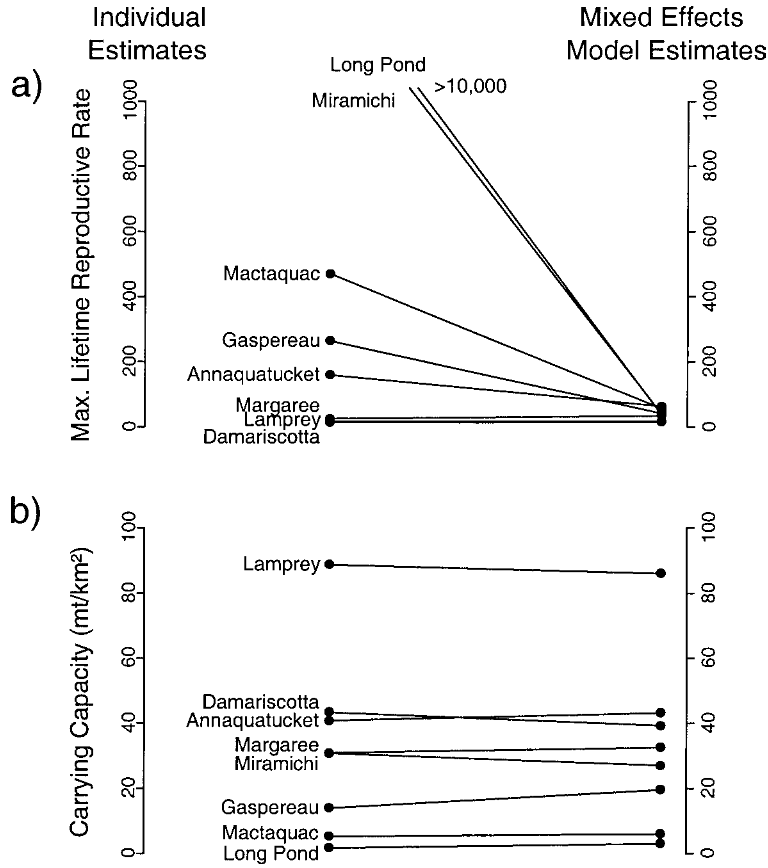

Figure 4.—A comparison of the estimates of the (a) maximum lifetime reproductive rate and the (b) habitat carrying capacity obtained from individual regressions on each alewife population and the empirical Bayes estimates obtained from the mixed model. mt = metric tons.

that of other species. In a meta-analysis of 239 fish populations, Myers et al. (1999) found that the maximum lifetime reproductive rate of a fish species ranged from about 2–25. These results are not directly comparable because Myers et al. (1999) used a Ricker model for their analysis, which produces estimates of the maximum reproductive rate that are lower than those of the Beverton–Holt model (Myers et al. 1999). While the Beverton–Holt model provided a better fit to our data than the Ricker model, our results are not precautionary with respect to model selection. Our estimate of the maximum lifetime reproductive rate may be high relative to other species, but it confirms that recruitment is related to spawner abundance in alewife and that spawning abundance targets must be met to ensure adequate recruitment in this species.

When estimated using the mixed-effects model, habitat carrying capacity still varied by a factor of about 25 times. This variability is similar to that determined for Atlantic cod *Gadus morhua* (more than 20 times; Myers et al. 2001) and coho salmon *Onchorhynchus kisutch* (about 10 times; Barrowman 2000). However, as discussed above, we cannot discount the possibility that some of this variability may result from the carrying capacity being underestimated for some populations.

We did not find evidence of depensation in the data. We were only able to estimate the depensation parameter for two of the eight populations we examined. These results, together with those of the mixed-effects model, suggest that the use of purely compensatory models is appropriate for alewife. However, this finding may also reflect the limits of the data. Given that the slope at the origin is not well determined in several of the data sets, detection of an inflection point in the spawner–recruit relationship near the origin is not very feasible for

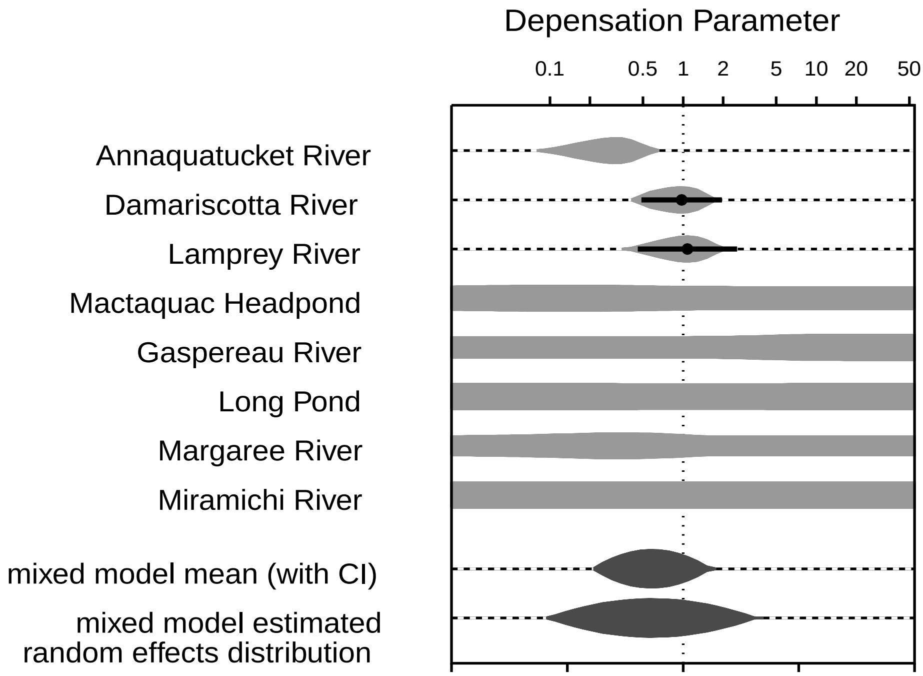

Figure 5.—A meta-analytic summary of the depensation parameter for eight alewife populations (see Figure 3 for details). A value of the depensation parameter greater than one is evidence of depensation, a value equal to one returns the Beverton–Holt model, whereas a value less than one suggests that a model with a sharper bend than the Beverton–Holt may be appropriate. Data for five of the populations contain little or no information about depensation when analyzed individually. CI = confidence intervals.

these populations. Therefore, we suggest a precautionary approach to the application of this result.

The meta-analysis of the dynamics of fish stocks can be readily extended to the estimation of biological reference points or other management parameters and provides a basis to evaluate the plausibility of the resulting estimates. Mixed-effects models, such as those used in our analysis, provide probability distributions for model parameters that can be incorporated into the assessment process using Bayesian methods. We suggest that when information about a population under study is compared with as many similar populations as possible, the resulting analysis and conclusions about the population under study are considerably enhanced.

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