Improving Removal-Based Estimates of Abundance by Sampling a Population of Spatially Distinct Subpopulations

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SUMMARY. A statistical modeling framework is described for estimating the abundances of spatially distinct subpopulations of animals surveyed using removal sampling. To illustrate this framework, hierarchical models are developed using the Poisson and negative-binomial distributions to model variation in abundance among subpopulations and using the beta distribution to model variation in capture probabilities. These models are fitted to the removal counts observed in a survey of a federally endangered fish species. The resulting estimates of abundance have similar or better precision than those computed using the conventional approach of analyzing the removal counts of each subpopulation separately. Extension of the hierarchical models to include spatial covariates of abundance is straightforward and may be used to identify important features of an animal’s habitat or to predict the abundance of animals at unsampled locations.

KEY WORDS: Depletion sampling; Empirical Bayes; Okaloosa darter; Removal sampling.

1. Introduction

Removal (or depletion) sampling is a well-known survey protocol used to estimate the abundance of demographically closed animal populations (Seber, 1982; Williams, Nichols, and Conroy, 2002). In this protocol, a population is sampled on separate occasions and the animals observed on each occasion are captured and removed from the population. Not surprisingly, removal-based methods of estimating abundance are popular in studies of exploited animals that are repeatedly sampled (as harvest) by hunters or fishermen.

A variety of models have been developed to estimate abundance from the sequence of counts observed in removal surveys (summarized in Williams et al., 2002, p. 320–325). The models differ primarily in whether they include auxiliary information that may be informative of temporal changes in capture rate. Perhaps the simplest of these models (Moran, 1951; Zippin, 1956) assumes that the probability of capture is identical in each sampling occasion. This assumption is more likely to be satisfied when the duration of the survey is kept short and when identical collection methods and effort are applied during each removal. Unfortunately, these desirable features of survey design become more difficult to achieve as the size of the region occupied by the population grows. A sample’s coverage also can decline with increases in the spatial extent of the population, particularly since practical considerations usually limit the total sampling effort. Inadequate coverage of a population can be detrimental to removal estimates of abundance because higher levels of accuracy and precision are generally attained as the proportion of the population observed in the sample increases (Williams et al., 2002).

One way of working around these difficulties is to view the population of animals as a collection of spatially distinct subpopulations (i.e., a metapopulation; Hanski and Simberloff, 1997) and to collect removal samples from each subpopulation selected for sampling. In this way, a relatively simple model of the capture process within each demographically closed subpopulation may be adequate. Of course, additional modeling is needed to specify a relationship that sensibly links the
subpopulation abundances with population abundance; otherwise the removals from each subpopulation would have to be analyzed separately, requiring an abundance parameter to be estimated for each subpopulation.

In this article, we develop a statistical modeling framework for estimating the abundances of spatially distinct subpopulations that are surveyed by removal sampling. We describe and illustrate several advantages of this framework over the conventional approach of separately analyzing the removal counts of each subpopulation. Although our removal-based estimators of abundance are not restricted to a particular species or population of animals, our efforts are strongly motivated by the need to monitor changes in abundance of an endangered fish species, the Okaloosa darter (Etheostoma okaloosae). This species occurs in only six stream systems that flow into Choctawhatchee Bay in northwest Florida. Okaloosa darters are relatively small fish (maximum size = 49 mm standard length) and are closely associated with the margins of streams to achieve the conservation goals of the Okaloosa darter recovery plan (U.S. Fish and Wildlife Service, 1998). In 1995, Eglin sponsored the development of a visual point count survey to monitor the abundance of Okaloosa darters at various locations and to evaluate the biological consequences of Eglin’s management actions at a specific subset of these locations. Although the number of darters observed in this survey has increased at locations where Eglin attempted habitat restoration, the survey’s design did not allow actual abundances to be estimated using methods that account for the imperfect detection of darters. Consequently, we have conducted removal sampling at various stream crossings on Eglin AFB to estimate the spatial variation in darter abundance and detection rates.

The remainder of this article is organized as follows. Section 2 begins with a description of the sampling protocol and the conventional method used to estimate abundance from removal counts. In Section 2.2, we develop a hierarchical modeling framework for estimating the abundances of subpopulations surveyed by removal sampling. This framework is illustrated in Section 2.3, where the Poisson and negative-binomial distributions are used to model variation in abundance among subpopulations and the beta distribution is used to model variation in capture rate among subpopulations. In Section 3, we apply these models in an analysis of data gathered during our survey of Okaloosa darters. Section 4 describes conclusions and possible extensions of our approach to more complex surveys.

2. Model Description

2.1 Sampling Protocol and Model of Counts

Suppose removal samples are taken from each of I spatially distinct subpopulations that constitute a representative sample of the entire population of animals. In addition, assume that the location and duration of the removals are selected to ensure that each of the subpopulations is demographically closed to changes in abundance due to births, deaths, immigration, or emigration. Although exchanges of animals between subpopulations are not permitted during the survey, this restriction is not permanent. Once sampling has been completed, animals can move freely among the different subpopulations without consequence to our estimators of abundance.

Let \( x_i \) denote the number of animals observed in the \( j \)th removal \((j = 1, \ldots, J_i)\) taken from the \( i \)th subpopulation \((i = 1, \ldots, I)\). We model the sequence of observed numbers of removals as a multinomial outcome \( (x_{i1}, x_{i2}, \ldots, x_{ij}, \ldots, x_{ijN_i}) \sim \text{Multinomial}(N_i, p_i) \), conditioning on the unknown number of animals \( N_i \) in the \( i \)th subpopulation and the conditional probabilities of capture \( p_i \) associated with the \( J_i \) removals. Let \( \theta_i \) denote the probability of capture during a single removal from the \( i \)th subpopulation; then \( p_i = \theta_i(1 - \theta_i)^{J_i - 1} \) specifies the probability of capture of animals during the \( j \)th removal, given that they have not been collected in earlier removals (Zippin, 1956). For now, we let \( \theta_i \) represent a constant capture parameter associated with subpopulation \( i \), recognizing that \( \theta_i \) can be easily formulated as a function of covariates to specify differences in capture among sites or removal times (Pollock, Hines, and Nichols, 1984; Gould and Pollock, 1997).

Under our modeling assumptions, the probability of a sequence of removal counts \( x_i \) from the \( i \)th subpopulation is

\[
f(x_i \mid N_i, \theta_i) = \frac{N_i!}{c_i(N_i - x_i)!} (1 - \theta_i)^{(N_i - x_i)} \times \prod_{j=1}^{J_i} \theta_i(1 - \theta_i)^{J_i - 1} x_{ij},
\]

(1)

where \( x_i = \sum_{j=1}^{J_i} x_{ij} \) is the total number of animals removed from subpopulation \( i \) and \( c_i = \prod_{j=1}^{J_i} x_{ij}! \). Zippin (1956) showed that estimates of \( N_i \) and \( \theta_i \) may be computed from \( x_i \) alone by treating (1) as a likelihood function to be maximized with respect to \( N_i \) and \( \theta_i \). For example, solving \( \partial f/\partial \theta_i = 0 \) yields

\[
\theta_i = \frac{x_i}{J_i(N_i - x_i) + \sum_{j=1}^{J_i} j x_{ij}}.
\]

(2)

Substituting this expression for \( \theta_i \) into (1) yields a profile-likelihood function for \( N_i \) that may be evaluated for admissible values of \( N_i (= x_i, x_i + 1, \ldots) \) to determine the maximum likelihood estimate \( \hat{N_i} \). Substituting this estimate of \( N_i \) back into (2) then yields the maximum likelihood estimate \( \hat{\theta_i} \) of the capture probability. Thus, it is entirely feasible to estimate the number of animals in each of the \( I \) subpopulations independently; however, there are both inferential and scientific benefits to be gained by combining the observed removals from all \( I \) subpopulations into a single modeling framework, which we describe in the following section.

2.2 A Hierarchical Framework for Estimating Abundance

2.2.1 Modeling subpopulation abundances. Suppose a probabilistic model is developed to specify variation in abundance
among the \( I \) spatially distinct subpopulations in the sample. Some of the differences in abundance may be attributed to systematic sources of variation among subpopulations (such as spatial variation or gradients in habitat quality); however, stochastic variation in abundances also may be present, particularly if the region where the subpopulations occur is reasonably homogeneous. Regardless of the cause(s) of variation in abundance among subpopulations, let a discrete density function \( g(N_i | \psi) \) specify a model of this variation, wherein \( \psi \) denotes a (possibly vector-valued) parameter. Obvious default choices for \( g \) are the Poisson and negative-binomial densities. For the moment, however, let \( g \) remain unspecified.

The model of site-specific removal counts (in \((1)\)) may be combined with the model of the spatial variation in abundance by integrating over the admissible values of \( N_i \) as follows:

\[
p(x_i | \psi, \theta_i) = \sum_{N_i=x_i}^{\infty} f(x_i | N_i, \theta_i)g(N_i | \psi).
\]

Therefore, \((3)\) specifies the marginal probability of observing a sequence of removal counts \( x_i \) from the \( i \)th subpopulation in terms of \( \theta_i \) and \( \psi \). To estimate these parameters, we assume that observations in different subpopulations are mutually independent and consider the following likelihood function:

\[
L(\psi, \{\theta_i\} | X) = \prod_{i=1}^{I} p(x_i | \psi, \theta_i),
\]

where \( X = (x_1, x_2, \ldots, x_j)^\prime \) denotes the matrix of observed numbers of animals removed during the survey. Our assumption of mutual independence is justified by the sampling design because animals can only be removed from a single subpopulation under the restriction of demographic closure. The marginal (or integrated) likelihood \( L \) can be maximized with respect to its parameters to compute the maximum likelihood estimates \( \hat{\psi} \) and \( \hat{\theta}_i \). Whether these estimates are of scientific interest depends on the nature and purpose of the study. For example, \( \psi \) can be formulated to specify an underlying relationship between subpopulation abundance and one or more spatial covariates (see Section 2.3), and this relationship is often of interest to ecologists. Here, we assume that primary interest lies in estimating the local abundance of each subpopulation and describe how inferences about \( N_i \) may be computed.

The density function \( g \), which specifies spatial variation in the abundances of subpopulations, can be regarded as a prior or mixing distribution for \( N_i \). Doing so allows us (via Bayes theorem) to express the conditional (on \( \psi \) and \( \hat{\theta}_i \)) posterior density for any admissible value of \( N_i \) as follows:

\[
\pi(N_i | X, \hat{\psi}, \hat{\theta}_i) = \frac{f(x_i | N_i, \hat{\theta}_i)g(N_i | \hat{\psi})}{p(x_i | \psi, \theta_i)}.
\]

Estimates of the \( i \)th subpopulation’s abundance based on \((5)\) are sometimes called empirical Bayes estimates (Carlin and Louis, 2000). Although summaries (mean, variance, or quantiles) of the conditional posterior distribution of \( N_i \) can be used to compute inferences about subpopulation abundance, these summaries fail to include uncertainty in the estimates of \( \psi \) and \( \theta_i \). Therefore, we recommend using \((5)\) to compute a parametric bootstrap approximation (Laird and Louis, 1987) of the marginal posterior density \( \pi(N_i | X) \), which integrates over uncertainty in estimates of model parameters. In Section 3.2, we show that this approach yields inferences that can be superior to those based on the profile-likelihood function described in Section 2.1.

2.2.2 Modeling subpopulation abundances and capture rates. In the previous section, each site-specific probability of capture \( \theta_i \) is assumed to be a fixed parameter, and no underlying model is used to characterize differences in capture rates among sites. Alternatively, suppose a probabilistic model is used to specify the variation in capture probabilities among the \( I \) sample locations. This model may include both systematic and stochastic sources of variation in capture. For the moment, however, let an unspecified density function \( h(\theta_i | \eta) \) represent the variation in capture among sites, where \( \eta \) denotes a (possibly vector-valued) parameter.

The model of site-specific removal counts developed in \((3)\) is easily extended to include variation in capture probabilities as follows:

\[
p(x_i | \psi, \eta) = \sum_{N_i=x_i}^{\infty} \left[ \int_0^1 f(x_i | N_i, \theta_i)h(\theta_i | \eta) d\theta_i \right] g(N_i | \psi).
\]

Therefore, \((6)\) specifies the marginal probability of observing a sequence of removal counts \( x_i \) from the \( i \)th subpopulation in terms of \( \psi \) and \( \eta \). To estimate these parameters, we assume that observations in different subpopulations are mutually independent and maximize the following integrated likelihood function: \( L(\psi, \eta | X) = \prod_{i=1}^{I} p(x_i | \psi, \eta) \). In Section 2.3, we show that particular choices of \( g \) and \( h \) allow the integrations in \((6)\) to be computed in closed form. When this is not feasible, direct summation over the discrete support of \( g \) and \( h \) or numerical (Romberg) integration (Carnahan, Luther, and Wilkes, 1969) over the compact support of \( h \) may be used.

Empirical Bayes estimates of the \( i \)th subpopulation’s abundance \( N_i \) may be computed (as described in Section 2.2.1) using the conditional (on \( \psi \) and \( \eta \)) posterior density of \( N_i \),

\[
\pi(N_i | X, \hat{\psi}, \hat{\eta}) \propto \frac{g(N_i | \hat{\psi})\int_0^1 f(x_i | N_i, \hat{\theta}_i)h(\theta_i | \hat{\eta}) d\theta_i}{p(x_i | \psi, \hat{\eta})},
\]

where \( \hat{\psi} \) and \( \hat{\eta} \) denote maximum likelihood estimates of the model parameters, and using parametric bootstrapping to account for the uncertainty in estimating \( \psi \) and \( \eta \).

2.3 Examples

In the previous section, density functions for modeling spatial variation in abundance or capture rate are specified only generally. Here, we describe reasonable default choices for \( g(N_i | \psi) \) and \( h(\theta_i | \eta) \).

2.3.1 A multinomial-Poisson mixture. A Poisson distribution, wherein \( [N_i | \lambda] \sim \text{Poisson}(\lambda) \) with \( \lambda \) denoting mean abundance among subpopulations, is perhaps the simplest default specification for the variation in abundance among subpopulations. This corresponds to a population of animals that are randomly distributed in space and aggregated (by choice of sampling locations) into subpopulations of size \( N_i \). The marginal probability of the sequence of counts \( x_i \) obtained by integrating \( N_i \) (in \((3)\)) to form a multinomial-Poisson mixture can be expressed in closed form:
Thus, the likelihood function (4) for this model is simply a product of Poisson densities, which has obvious computational advantages for the maximization of \( L \). In practice, the model parameters \( \lambda \) and \( \theta_i \) are typically transformed (using \( \log \lambda = \alpha \) and \( \log (\theta_i/(1 - \theta_i)) = \beta_i \)) to ensure that estimates of the parameters are confined to their admissible ranges without requiring constraints during optimization. These transformations are also convenient choices for extending the model to include additional, systematic sources of variation in abundance or capture probability. For example, if site- or removal-time-specific covariates (say, \( v_{ij} \)) are available, a Poisson regression formulation \( \log \lambda_i = u_i \alpha \) can be used, wherein \( L \) is maximized with respect to \( \alpha \). Similarly, if site- or removal-time-specific covariates (say, \( e_{ij} \)) of capture probability are available, a logistic regression formulation \( \log (\theta_{ij}/(1 - \theta_{ij})) = v_{ij} \beta \) can be used, wherein \( L \) is maximized with respect to \( \beta \).

Conventional methods may be used to assess the adequacy of this model owing to the closed form of the multinomial-Poisson mixture density. The deviance statistic \( G^2 \) (Agresti, 2002) for comparing the magnitudes of expected and observed numbers of animals removed is a sum of site-specific residual deviances, \( G^2 = \sum_{i=1}^{I} G_i^2 \), where

\[
G_i^2 = 2 \sum_{j=1}^{J_i} (x_{ij} - N_i \lambda_i) \left[ \lambda_i \left( 1 - \theta_i \right)^{j-1} + x_{ij} \left[ \log x_{ij} - \log(\lambda_i \left( 1 - \theta_i \right)^{j-1}) \right] \right].
\]

In sufficiently large samples, the model’s goodness-of-fit may be ascertained by comparing \( G^2 \) with its asymptotic \( \chi^2 \) distribution, where \( \nu = \sum J_i - I - 1 \).

### 2.3.2 A multinomial-negative binomial mixture

In many (perhaps most) natural populations of animals, spatial randomness is unlikely. Habitat preferences of animals tend to induce aggregation of individuals in the vicinity of favorable habitats, leading to an overdispersed distribution of subpopulation abundances. Territorial behaviors, on the other hand, have the opposite (repulsive) effect and can produce subpopulation abundances that are underdispersed relative to the Poisson. The spatial scales of habitat differences and behavioral interactions also are important in determining the amount of variation in subpopulation abundance.

Suppose our removal sample of the population comprises subpopulations whose abundances are thought to be overdispersed. In the absence of spatial covariates that might be used to model this overdispersion, the negative-binomial distribution provides a reasonable starting point for constructing a model of the subpopulation abundances. Thus, we consider the following discrete density function

\[
g(N_i | \lambda, \varepsilon) = \frac{\Gamma(N_i + \varepsilon^{-1})}{\Gamma(\varepsilon^{-1}) N_i! \Gamma(1 + \varepsilon)} \left( N_i \varepsilon \lambda \right)^N_i \left( 1 + \varepsilon \lambda \right)^{-1-N_i},
\]

which implies \( E(N_i) = \lambda \) and \( \text{Var}(N_i) = \lambda + \varepsilon \lambda^2 \) (Lawless, 1987). The overdispersion parameter \( \varepsilon \) is positive (by definition); however, a limiting (degenerate) form of the negative binomial density occurs for \( \varepsilon = 0 \), where \( N_i \sim \text{Poisson}(\lambda) \). Thus, (10) provides a natural (hierarchical) extension of the multinomial-Poisson mixture described in the previous subsection. Moreover, \( \lambda \) also can be formulated as a function of site-specific covariates (as described earlier) to model additional, systematic variation in abundance among subpopulations.

The marginal probability of the sequence of counts \( x_i \) under the multinomial-negative binomial mixture cannot be expressed in closed form. Therefore, while evaluations of (3) and (4) (where \( \psi = (\lambda, \varepsilon) \) are feasible, they can be computationally intensive. Nonetheless, computing maximum likelihood estimates of this model’s parameters is relatively straightforward.

Methods for assessing the adequacy of this model are, however, less obvious. This difficulty is common in hierarchical models composed of latent parameters. Here, we propose a possible solution. Suppose counterfactually that \( N_i \) is known; then the contribution of the \( i \)th site to the total deviance has the usual form of a multinomial deviance

\[
G^2(N_i) = 2 \sum_{j=1}^{J_i} \left( N_i x_{ij} \log \frac{N_i x_{ij}}{N_i (1 - \theta_i)^j} \right) + \sum_{j=1}^{J_i} x_{ij} \left[ \log x_{ij} - \log \left( N_i \theta_i (1 - \theta_i)^{j-1} \right) \right],
\]

where \( G^2(N_i) \) is used to denote explicitly the dependence on \( N_i \). However, \( N_i \) is not an unknown constant parameter in our model; therefore, we compute the \( i \)th site’s contribution to \( G^2 \) as an expectation that integrates over the conditional posterior distribution of \( N_i \) as follows:

\[
E_x \left[ G^2(N_i) \right] = \sum_{N_i=x_i}^{\infty} G^2(N_i) \pi(N_i | \lambda, \varepsilon, \theta_i).
\]

The total deviance is computed by summing the contributions from all sites: \( G^2 = \sum_{i=1}^{I} E_x \left[ G^2(N_i) \right] \). Although we have not derived a limiting distribution of this statistic for use in tests of goodness-of-fit, parametric bootstrapping may be used to compute an approximation. In this procedure, an arbitrarily large number of data matrices \( X \) are randomly simulated using the model structure and the maximum likelihood estimates of its parameters. The model is then fitted to each of these simulated data sets and a corresponding \( G^2 \) statistic is computed. The distribution of these simulated statistics may be regarded as an approximate reference distribution of the deviance and used to assess goodness-of-fit by determining whether the actual deviance (based on the observed data) appears to be consistent with the simulated distribution of deviances.

### 2.3.3 A multinomial-Poisson-beta mixture

The multinomial-Poisson mixture (Section 2.3.1) is easily extended to model spatial variation in capture rates. Suppose a beta distribution with density \( h \) is used to model the variation in capture rates among sites:

\[
h(\theta_i | \mu, \tau) = \frac{\Gamma(\tau)}{\Gamma(\tau \mu) \Gamma(\tau (1 - \mu))} \theta_i^{\mu - 1} (1 - \theta_i)^{\tau (1 - \mu) - 1},
\]
wherein \( E(\theta_i | \mu, \tau) = \mu \) and \( \text{Var}(\theta_i | \mu, \tau) = \mu(1 - \mu)/(\tau + 1) \). Thus, \( \mu \) specifies the average probability of capture among sites, and \( \tau \) parameterizes the similarity (inverse of variation) in site-specific capture probabilities.

The marginal probability of the sequence of removal counts \( x_i \) for this model is easily obtained by exchanging the order of integration in (6) and exploiting the closed form of (8):

\[
p(x_i | \lambda, \mu, \tau) = \int_0^1 p(x_i | \lambda, \theta_i) h(\theta_i | \mu, \tau) d\theta_i.
\]

Although numerical integration is required to evaluate (14), maximizing the likelihood function of this model is relatively straightforward. In practice, the model parameters \( \mu \) and \( \tau \) are typically transformed (using \( \log(\mu/(1 - \mu)) = \beta \) and \( \log \tau = \phi \)) to ensure that estimates of the parameters are confined to their admissible ranges without requiring constraints during optimization. These transformations are also convenient choices for extending the model to include additional, systematic sources of variation in capture probability. For example, if site-specific covariates (say, \( v_i \)) of capture probability are available, a beta-binomial regression formula can be used, wherein \( L \) is maximized with respect to \( \beta \). In the absence of such covariates, the multinomial-Poisson-beta mixture specifies an intermediate model that lies hierarchically between two multinomial-Poisson models, one with site-specific (but fixed) capture probabilities \( \theta \) and another with identical capture probabilities at all sites (\( \theta_i = \theta, \forall i \)).

Assessing the adequacy of the multinomial-Poisson-beta mixture for a particular set of removal counts is difficult, in part because the integral in (14) cannot be evaluated analytically. However, we can apply the approach used earlier (Section 2.3.2) to derive an expected deviance statistic for measuring goodness-of-fit.

2.3.4 A multinomial-negative binomial-beta mixture. The multinomial-negative binomial mixture (Section 2.3.2) can be extended to model spatial variation in capture rates by using the beta mixing distribution. However, in this case, we obtain computational savings by evaluating the integral in (6) analytically as follows:

\[
g(x_i | N_i, \mu, \tau)
\]

\[
= \int_0^1 f(x_i | N_i, \theta_i)h(\theta_i | \mu, \tau) d\theta_i
\]

\[
= N_i! \cdot c_i(N_i - x_i)! \cdot B \left( \tau \mu + x_i, \tau(1 - \mu) + J_i(N_i - x_i) - x_i + \sum_{j=1}^{J_i} jx_i \right) / B(\tau \mu, \tau(1 - \mu)) \quad (15)
\]

where \( B(\cdot, \cdot) \) denotes the beta function. Thus, the marginal probability of the sequence of removal counts \( x_i \) is computed by summation as follows:

\[
p(x_i | \lambda, \varepsilon, \mu, \tau) = \sum_{N_i = x_i}^\infty q(x_i | N_i, \mu, \tau)g(N_i | \lambda, \varepsilon). \quad (16)
\]

Maximizing the likelihood function of this model, although computationally intensive, is straightforward.

Assessing the adequacy of this model for a particular set of removal counts can be accomplished by deriving an expected deviance statistic (as described in Section 2.3.2), wherein each site’s contribution is computed as an expectation that integrates over the joint conditional posterior density of \( N_i \) and \( \theta_i \). Details are available upon request.

3. A Removal-Based Survey of Okaloosa Darters

3.1 Collection Methods

In late summer 2003, five stream crossings at Eglin AFB in northwestern Florida were selected to assess the effectiveness of visually surveying a population of Okaloosa darters. At each stream crossing, the left and right margins of two 20-m sections of stream (upstream and downstream) were visually inspected by experienced biologists using mask and snorkel. Using a clear plastic net (20 cm wide × 15 cm high × 40 cm deep with 1-mm mesh screen), each biologist captured all darters encountered in successive passes of each site taken in an upstream direction. Darters were counted as they were transferred to buckets onshore for temporary holding. Successive removals were taken until either one or zero darters was observed. This required three to five passes and 1 to 4 hours for each stream margin and section.

Stream margins characteristically had tree roots, emergent vegetation, and detritus ranging from logs to flocculent debris. The center of the stream bottom typically was a broad expanse of sand and small quartzite gravel. Therefore, we believe that during the survey there was minimal opportunity for darters to move between left and right margins (separated by 3.2–6.5 m) or between upstream and downstream sections (separated by 8–23 m) at each stream crossing. Consequently, the darters observed at different stream margins and sections.

| Table 1 |
| Number of darters removed at each of 20 sampling sites |

<table>
<thead>
<tr>
<th>Stream crossing</th>
<th>Stream section</th>
<th>Stream margin</th>
<th>Site number</th>
<th>Removal number</th>
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<td>9 3 2 0 –</td>
</tr>
<tr>
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<td>downstream</td>
<td>right</td>
<td>2</td>
<td>33 5 3 2 0</td>
</tr>
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<td>upstream</td>
<td>left</td>
<td>3</td>
<td>14 2 1 – –</td>
</tr>
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<td>upstream</td>
<td>right</td>
<td>4</td>
<td>4 12 5 1 –</td>
</tr>
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<td>left</td>
<td>5</td>
<td>24 11 9 8 1</td>
</tr>
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<td>right</td>
<td>6</td>
<td>25 9 1 – –</td>
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<td>left</td>
<td>17</td>
<td>22 5 8 2 0</td>
</tr>
<tr>
<td>Swift</td>
<td>upstream</td>
<td>right</td>
<td>18</td>
<td>15 4 1 – –</td>
</tr>
<tr>
<td>Swift</td>
<td>downstream</td>
<td>left</td>
<td>19</td>
<td>19 6 1 – –</td>
</tr>
<tr>
<td>Swift</td>
<td>downstream</td>
<td>right</td>
<td>20</td>
<td>16 11 3 1 –</td>
</tr>
</tbody>
</table>
are treated as demographically closed subpopulations in our analysis.

3.2 Data Analysis
The total number of darters removed from each of the 20 subpopulations ranged from 14 to 53 fishes (Table 1). As expected, the number of fish removed generally declined in successive removals from each subpopulation of darters. It can be argued that our sampling protocol, wherein darters were removed at each site until either 1 or 0 fish was caught, leaves little to estimate because the abundance at each site essentially equals the total number of fish removed at that site. To evaluate the estimators of abundance, we therefore analyzed a subset of the removal data shown in Table 1, using only the first three removals at each site. In other words, darters captured in the final one or two passes made at sites with four or five removals were ignored in the analysis.

The multinomial-Poisson and multinomial-negative binomial mixtures were both fitted to the removal counts, while allowing for either constant or site-specific (but fixed) probabilities of capture. Table 2 contains a comparison of these fits (models 1, 3, 4, and 6). Likelihood-ratio comparisons of models with and without site-specific capture parameters suggest that capture rates differ significantly among sites, regardless of whether the variation in abundances is modeled as Poisson ($P = 0.000003$) or negative binomial ($P = 0.0003$). Likelihood-ratio comparisons of models that contain site-specific capture parameters but differ in their formulation of variation in subpopulation abundance (i.e., Poisson vs. negative binomial) cannot be used because the heterogeneity parameter lies on a boundary ($\varepsilon = 0$) under the assumptions of the null (Poisson) model (Lawless, 1987). However, the reduction in residual deviance $G^2$ and corresponding improvement in fit obtained with the negative binomial provides evidence in favor of this overdispersed model of subpopulation abundances.

Two hierarchical intermediates (models 2 and 5 in Table 2) of the models with fixed capture parameters also were fitted to the removal counts. A comparison of the deviances of these two models suggests that the negative binomial model of subpopulation abundances provides a better fit to the data than the Poisson model, supporting our earlier conclusion based on a comparison of models 3 and 6. Among the models that specify negative-binomial variation in abundance, both model 6 (with fixed, site-specific capture parameters) and model 5 (with stochastically varying, site-specific capture parameters) appear to provide an adequate fit to the removal data. In the interest of parsimony, we selected the multinomial-negative binomial-beta mixture (model 5) as a basis for inference.

Using this model, the estimated mean probability of capture is $\hat{\mu} = 0.61$ and the estimated mean number of darters (per site) is $\hat{\lambda} = 28.8$. Figure 1 illustrates the expected levels of variation in abundance and capture probability among the spatially distinct subpopulations of darters, given the maximum likelihood estimates $\hat{\tau} = 14.2$ and $\hat{\varepsilon} = 0.08$. In Table 3, we compare empirical Bayes estimates of site-specific abundance of darters based on the multinomial-negative binomial-beta mixture with maximum likelihood estimates obtained by fitting the conventional removal model (Zippin, 1956) to each site separately. Although the abundance estimates of these two models generally agree (except for site 4), a comparison of their 95% confidence intervals indicates that the hierarchical model's estimates can be much more precise (e.g., sites 4, 5, 9, 10, 12, 15, 17, 20). This increase in precision occurs because each site-specific abundance is estimated from the hierarchical model's parameter estimates ($\hat{\lambda}$, $\hat{\varepsilon}$, $\hat{\mu}$, and $\hat{\tau}$), which depend on the data observed at all sites. In this way, each site's estimate of $N_i$ borrows strength from the data observed

![Figure 1](image-url). Estimated variation in probability of capture and abundance among spatially distinct subpopulations, given maximum likelihood estimates of the parameters of the multinomial-negative binomial-beta mixture.
Improving Removal-Based Estimates of Abundance

Table 3
Comparison of model-based estimates of site-specific abundance of darters. Total number of darters captured in the first three removals at site i is denoted by $x_i$.

<table>
<thead>
<tr>
<th>Site</th>
<th>$x_i$</th>
<th>Single-site model (Zippin, 1956)</th>
<th>Hierarchical model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Maximum likelihood estimate</td>
<td>Empirical Bayes estimate</td>
</tr>
<tr>
<td></td>
<td></td>
<td>95% Profile-likelihood interval</td>
<td>95% Empirical Bayes confidence interval</td>
</tr>
<tr>
<td>1</td>
<td>14</td>
<td>14</td>
<td>16.3</td>
</tr>
<tr>
<td>2</td>
<td>41</td>
<td>41</td>
<td>42.1</td>
</tr>
<tr>
<td>3</td>
<td>17</td>
<td>17</td>
<td>18.0</td>
</tr>
<tr>
<td>4</td>
<td>21</td>
<td>206</td>
<td>27.3</td>
</tr>
<tr>
<td>5</td>
<td>44</td>
<td>52</td>
<td>48.8</td>
</tr>
<tr>
<td>6</td>
<td>35</td>
<td>35</td>
<td>36.3</td>
</tr>
<tr>
<td>7</td>
<td>24</td>
<td>24</td>
<td>25.2</td>
</tr>
<tr>
<td>8</td>
<td>32</td>
<td>33</td>
<td>34.1</td>
</tr>
<tr>
<td>9</td>
<td>21</td>
<td>22</td>
<td>23.8</td>
</tr>
<tr>
<td>10</td>
<td>14</td>
<td>14</td>
<td>16.7</td>
</tr>
<tr>
<td>11</td>
<td>15</td>
<td>15</td>
<td>15.6</td>
</tr>
<tr>
<td>12</td>
<td>16</td>
<td>17</td>
<td>19.0</td>
</tr>
<tr>
<td>13</td>
<td>29</td>
<td>29</td>
<td>29.8</td>
</tr>
<tr>
<td>14</td>
<td>40</td>
<td>40</td>
<td>41.4</td>
</tr>
<tr>
<td>15</td>
<td>21</td>
<td>22</td>
<td>23.8</td>
</tr>
<tr>
<td>16</td>
<td>34</td>
<td>35</td>
<td>36.4</td>
</tr>
<tr>
<td>17</td>
<td>35</td>
<td>39</td>
<td>38.6</td>
</tr>
<tr>
<td>18</td>
<td>20</td>
<td>20</td>
<td>21.2</td>
</tr>
<tr>
<td>19</td>
<td>26</td>
<td>26</td>
<td>27.2</td>
</tr>
<tr>
<td>20</td>
<td>30</td>
<td>32</td>
<td>33.1</td>
</tr>
</tbody>
</table>

in other sites, and this is manifest as an overall improvement in site-specific inferences.

The potential benefits of hierarchical modeling are, in fact, understated in our analysis of the darter removals. We completed a simulation experiment to illustrate further the inferential advantages of estimating site-specific abundances with the empirical Bayes estimator. In each simulation experiment, 100 random samples of removal counts were computed using the multinomial-negative binomial-beta mixture (Section 2.3.4) as a data-generating model. Each sample included a sequence of three removal counts at each of I = 20, 40, or 80 sites. Maximum likelihood estimates of the model parameters were used ($\hat{\mu} = 0.61$, $\hat{\tau} = 14.2$, $\hat{\lambda} = 28.8$, $\hat{\varepsilon} = 0.08$) in half of the simulation experiments; in the other half $\mu$ was assigned the value of 0.43 (70% of $\hat{\mu}$) to reduce the average proportion of animals removed per site. The hierarchical (data-generating) model and the conventional removal model (Zippin, 1956) were fitted to each of the simulated samples and used to estimate the mean abundance among subpopulations as follows: $\hat{N} = (\sum_{i=1}^{I} \hat{N}_i)/I$, where $\hat{N}_i$ denotes a model-based estimate of $N_i$. The two different estimators of abundance were compared by evaluating simulation-based estimates of their mean squared error ($\hat{N} - N$)$^2$ and bias ($\hat{N} - N$) in estimating the true mean abundance $\hat{N}$. The results of the simulation experiments (Table 4) indicate that the empirical Bayes estimator can be considerably more precise than the conventional removal estimator. Mean squared errors of the latter are one or two orders of magnitude higher than those of the empirical Bayes estimator at each of the three sample sizes. Furthermore, estimates of abundance computed using Zippin’s (1956) method appear to be positively biased (especially when $\mu = 0.43$), whereas the empirical Bayes estimates are nearly unbiased.

At a referee’s request we completed a second simulation study to illustrate the performance of the empirical Bayes estimator in circumstances where the proportion of animals removed is much lower than that estimated for the Okaloosa darter. These simulations were conducted as described in the previous paragraph except that the multinomial-Poisson

Table 4
Comparison of abundance estimators using simulation-based estimates of their MSE and bias. Each simulation included 100 randomly generated samples of removal counts. The parameters, $\mu$, $\tau$, $\lambda$, and $\varepsilon$, of the multinomial-negative binomial-beta mixture (Section 2.3.4) were used to generate a sequence of three removal counts at each of 20, 40, or 80 sites. Maximum likelihood estimates of these parameters were used in half of the simulation experiments; in the other half $\mu$ was assigned the value of 0.43 to reduce the average proportion of animals removed per site (denoted by $p$).

<table>
<thead>
<tr>
<th>$\mu$</th>
<th>Number of sites</th>
<th>MSE</th>
<th>Bias</th>
<th>MSE</th>
<th>Bias</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.61</td>
<td>20</td>
<td>8.97</td>
<td>0.20</td>
<td>0.52</td>
<td>-0.04</td>
</tr>
<tr>
<td>0.61</td>
<td>40</td>
<td>4.64</td>
<td>0.40</td>
<td>0.24</td>
<td>-0.07</td>
</tr>
<tr>
<td>0.61</td>
<td>80</td>
<td>1.61</td>
<td>0.29</td>
<td>0.13</td>
<td>0.05</td>
</tr>
<tr>
<td>0.43</td>
<td>20</td>
<td>116.89</td>
<td>6.55</td>
<td>3.57</td>
<td>0.08</td>
</tr>
<tr>
<td>0.43</td>
<td>40</td>
<td>64.27</td>
<td>4.59</td>
<td>1.86</td>
<td>0.01</td>
</tr>
<tr>
<td>0.43</td>
<td>80</td>
<td>61.67</td>
<td>6.43</td>
<td>0.90</td>
<td>-0.08</td>
</tr>
</tbody>
</table>
Comparison of abundance estimators using simulation-based estimates of their MSE and bias. Each simulation included 1000 randomly generated samples of removal counts. The parameters, $\lambda$ and $\theta_i$, of the multinomial-Poisson mixture (Section 2.3.1) were used to generate a sequence of three removal counts at each of 200 sites. Each $\theta_i$ was assigned the value of 0.1565691 to ensure that only 40\% of animals were removed from each site (on average). $p_\infty$ denotes the average proportion of sites for which the single-site model’s estimate of $N$ was $\infty$. MSE and bias of the single-site model’s estimator were computed by excluding sites for which $N$ was not estimable (i.e., sites with no captures or sites for which $N = \infty$).

<table>
<thead>
<tr>
<th>$\lambda$</th>
<th>Proportion of sites with no captures</th>
<th>Single-site model</th>
<th>Hierarchical model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$p_\infty$</td>
<td>MSE</td>
<td>Bias</td>
</tr>
<tr>
<td>5</td>
<td>0.135</td>
<td>0.057</td>
<td>6.5</td>
</tr>
<tr>
<td>10</td>
<td>0.018</td>
<td>0.105</td>
<td>22.3</td>
</tr>
<tr>
<td>20</td>
<td>$3.3 \times 10^{-4}$</td>
<td>0.144</td>
<td>45.5</td>
</tr>
</tbody>
</table>

mixture (Section 2.3.1) was used as a data-generating model and removal counts were simulated at $I = 200$ sites. Site-specific capture probabilities were assigned a value of 0.1565691 to ensure that the expected proportion of animals removed per site was only 0.4. In addition, the mean abundance parameter was assigned relatively low values ($\lambda = 5, 10, 20$) to further challenge the estimators of site-specific abundance. In the simulated data, it was not uncommon for there to be a substantial proportion of sites without any captured animals (i.e., $x_i = 0$). The highest proportion of these sites (0.135) occurred when mean abundance was lowest (Table 5). At these sites the conventional removal model cannot provide an estimate of $N_i$ or $\theta_i$. The empirical Bayes approach, on the other hand, does provide an abundance estimate for these sites as long as animals have been captured and removed at a sufficient number of the other sites. Our simulated samples also contained sites where the number of animals observed in successive removals did not decline. Fitting the conventional removal model to these removal sequences produces a well-known deficiency of Zippin’s estimator, that is $N = \infty$. As before, the empirical Bayes estimator does not suffer from these estimation problems provided adequate data exist at the other sites.

The second simulation study was intentionally designed to make the estimation of site-specific abundance difficult. The inferential advantages of the empirical Bayes estimator (improved estimability, lower bias, and lower MSE) are immediate consequences of the hierarchical modeling framework. Information from other sites can be used to improve inferences at a particular site, even when that site’s information alone does not provide an adequate inference. The key, of course, is collecting data from enough sites to make the leveraging of information possible.

4. Discussion

Natural populations of animals often are composed of spatially distinct subpopulations (Hanski and Simberloff, 1997). From a statistical point of view, this spatial structure can be exploited in terms of both sampling design and data analysis to improve inferences related to subpopulation abundances and to identify important sources of variation in those abundances. For example, in our removal survey of Okaloosa darters, sites were selected to be representative of those thought to provide favorable habitat to these fish. Combining the removals of darters observed at different sites into a common modeling framework considerably reduces the uncertainty in estimates of subpopulation abundance at some sites (Table 3). In addition, inferences related to subpopulation abundance are computed using the full conditional posterior density (5), as opposed to relying on the asymptotics that underlie a profile-likelihood-based interval.

The framework that we describe also provides a model-based specification of the spatial variation in abundance. Covariates that are thought to be informative of site-specific differences in abundance, or of site- or time-specific differences in capture rate, are easily included (see Section 2.3). This type of modeling can be used to identify important features of an animal’s habitat or to predict the abundance of animals at unsampled locations (provided the relevant covariates are available for those locations). For example, such predictions might be based on features of the landscape included in geographic information systems (GIS), which are widely available. The hierarchical framework that we have used to model spatial variation in abundance is a natural extension of single-site removal models. Similar extensions have been developed for surveys that use other sampling protocols, such as single-observer point counts (Dodd and Dorazio, 2004; Royle, 2004) and distance samples (Royle, Dawson, and Bates, 2004).

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REFERENCES


