

Multiple-Species Models for True Abundances Allowing for Heterogeneity of Capture Between and Within Species

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SUMMARY. Probabilities for *observance* (capture) of individuals often differ between species. Previous research involving species' abundances, diversity, and evenness have largely ignored this fact. In this paper, we allow for unknown differences in capture probabilities through use of finite mixture nonparametric modeling of species true abundances and of their individuals' capture probabilities. This modeling also allows us to develop diversity and evenness measures based on *true* abundances of species. A fisheries removal experiment serves as a motivating example. We also evaluate our methods on several test data sets for both the removal setting and the capture-recapture setting.

KEY WORDS: Species abundances; Finite mixture models; Capture-recapture; Diversity and evenness measures.

1. Introduction

In order to study and manage an ecological community, it is important to obtain substantial practical and theoretical information on its species' abundances. Historically, Fisher et. al. (1943), Preston (1948), Ludwig and Reynolds (1988), and others have proposed different parametric distributions for species' *observed* abundances. Norris and Pollock (1998) presented a Poisson finite mixture model for species' observed abundances. Under appropriate sampling conditions, we can extend this Norris and Pollock (1998) work to construct a Poisson finite mixture model for the species' *true* abundances. This is a major advance since probabilities for observance often differ both between and within species, and making inferences about the *true*, rather than the observed, abundances is much preferred. In this paper, we develop such an extension.

Since a species abundance is a *count* of individuals within a species, it should be noted that several other fields of study, most notably econometrics (e.g. Cameron and Trivedi (1998)), have conducted substantial research in count data models. Much of that research has involved counts in a regression setting. However, our research involves counts of individuals within groups (species) with the groups' count means coming from a common finite distribution. Importantly our setting allows individuals to only have a chance of being observed, and this chance can vary between and within groups.

In Section 2, we begin by discussing a motivating example from a fisheries setting. We also utilize this example to introduce notation and provide a conceptual framework. In Section 3, we present the details of our model and discuss its more general applicability. In Section 4, we show how our results can be used to construct diversity and evenness measures based on true

abundances. In Section 5, we present the results from utilizing our model on the motivating example as well as test data sets. Section 6 concludes the paper with a general discussion.

2. Ecological Illustration and Notation

In May 2002, Dr. Thomas Kwak and colleagues conducted a fisheries study in a sector of the Lumbee River in the eastern part of North Carolina, USA. For each of three passes on the same day, electrofishing was used to “remove” individual fish of differing species from the capturable population. Therefore, separately for each of the species, we have a three-period closed population removal model with similar periods and perhaps heterogeneity in the capture probabilities between individuals; these models are often labeled M_{bh} . In this paper, we model the collective data over all species; this allows interesting ecological inferences, e.g. measures of species diversity and evenness. In addition, since there are multiple capture periods, we can make inferences about capture probabilities and thus can make inferences about *true* species’ abundances rather than just observed species’ abundances. Our methods are equally applicable for the non-removal capture-recapture setting, often labeled as M_h ; see the end of Section 3.1.

Basic Notation and Assumptions

- N is the total number of species existing in the (original capturable) population
- Y_l is the true abundance of existing species l of the population. Note that Y_l can not be zero since species l exists.
- Given λ_l , Y_l comes from a zero-truncated Poisson (λ_l) distribution.

[Note: since Y_l is a *total* abundance over the “region”, then even if the “region” is quite diverse, it may still be reasonable to assume that $(Y_l | \lambda_l)$ is zero-truncated Poisson because the sum (accumulated total) of independent Poissons is Poisson; see Section 6 for additional discussion.]

- The λ ‘s of the different species can differ, but they were each generated from a common unknown finite distribution; label it as F . Let B denote the number of support points of F and label these points as: $\lambda_1, \lambda_2, \dots, \lambda_B$ with respective weights of u_1, u_2, \dots, u_B . Thus (unconditionally) each Y_l comes from a Poisson (F) mixture distribution.

- Let p_{lm} denote the probability that individual fish m of species l is captured on a particular period, if it is still in the capturable population.

- For a given λ , the p_{lm} ‘s can differ but they were each generated from an unknown finite distribution, possibly depending on λ ; label it as D_λ . Thus each D_{λ_b} has, say, W points of support labeled as $p_{b1}, p_{b2}, \dots, p_{bW}$ with corresponding weights $r_{b1}, r_{b2}, \dots, r_{bW}$. It should be emphasized that our model allows the p ’s to differ both between and within species.

- Let t denote the number of capture periods and

- v denotes a particular capture history (e.g. $v = 001$ means that the individual was not (0) captured on either the first or second period but it was (1) captured on the third period).

- $k_l(v)$ denotes the number of individuals of species l that had capture history v .

- s_l denotes the (total) number of individuals of species l that were detected in the study.

- The data consists of the following: separately for each species, the numbers of its individuals which had the respective observed capture histories; i.e. the set of $k_l(v)$ ’s over all observed species l and for all $v \neq \underline{0}$.

Lumbee River Fisheries Example

The Lumbee River fisheries data set is shown in Table 1. For specified *numbers* B and W of finite mixture support points, maximum likelihood estimates of the entire set of parameters were obtained through use of Splus/R-based programs, which are available from the authors. Multiple choices for B and W as well as submodels were examined in order to help determine the most appropriate model. Details of results are discussed in Section 5, but for now we mention that the “best” model for this data set appears to be the model with $B = 4$, $W = 1$, and a single common p . The corresponding mle estimates are: $N = 23$; (for F) the 4 lambda values of (2.30, 10.21, 37.72, 99.46) with respective weights of (0.29, 0.37, 0.21, 0.13) ; (for D) the one common p being 0.44. From these, mle’s of diversity and evenness measures on species *true* abundances can be easily computed (as demonstrated in Section 4).

Based on our mle results, some practical inferences for the May 2002 Lumbee River setting are as follows: at least one individual from nearly all of this population’s capturable species were caught sometime during this study (since mle of N is the *observed number of species*, S); here, capture probabilities do not appreciably differ between species or within species; diversity of the species’ true abundances is moderate, and Poisson means of true abundances appreciably differed between species.

3. Model development

3.1 Full model likelihood

In Section 2, we defined many of the individual components of our model. Now we further develop our model. Recall that N is the (unknown) number of species in the community; S is

the number of species observed in the study; Y_l is the abundance of existing species l , and $k_l(v)$ denotes the number of individuals of species l with capture history v . Thus, the entire data for a given species l is the set of $k_l(v)$ over all $v \neq 0$; label this as A_l ; (The subscript is dropped when referring to a generic species.) Thus assuming independence of species, the full likelihood over all existing species follows a multinomial distribution with a possible cell being a potential set of values for the $k(v)$'s over all v . Thus, the full likelihood can be expressed as

$$L \propto \binom{N}{S} \left(\prod_{l=1}^S P(A_l) \right) \cdot (P(A_{none}))^{(N-S)} \quad (1)$$

where the index for the species now lists the detected species first, “ A_{none} ” refers to no individuals being observed for a given species, and proportionality is with respect to the model's parameters, which for a given B and W are: N , the λ_b 's, the u_b 's, the p_{bw} 's, and the r_{bw} 's.

To compute $P(A_l)$ and $P(A_{none})$, it is useful to vectorize some of the notation of Section 2. In particular, let $\delta_b \equiv (N, \lambda_b, p_{b1}, p_{b2}, \dots, p_{bW}, r_{b1}, r_{b2}, \dots, r_{bW})$. Then for $l \leq S$, we have that

$$P(A_l) = \sum_{b=1}^B P(A_l | \delta_b) \cdot P(\delta_b) = \sum_{b=1}^B u_b \sum_{Y_l = s_l}^{\infty} [P(A_l \text{ and } Y_l | \delta_b)] =$$

$$\sum_{b=1}^B u_b \sum_{y_l = s_l}^{\infty} [P(A_l | Y_l \text{ and } \delta_b) P(Y_l | \delta_b)]$$

Note that the first probability in the final bracket is a multinomial probability (with cells being the capture histories, the v 's) while the latter probability is a zero-truncated Poisson probability.

Thus, we have (for $l \leq S$), that $P(A_l)$ is proportional to

$$\sum_{b=1}^B u_b \sum_{Y_l=s_l}^{\infty} \frac{(Y_l)!}{(Y_l - s_l)!} \left\{ \left[\pi \left\{ \sum_{v \neq 0} \sum_{w=1}^W r_{bw} c_{p_{bw}}(v) \right\} \right]^{k_l(v)} \left[\sum_{w=1}^W r_{bw} c_{p_{bw}}(0) \right]^{(Y_l - s_l)} \cdot \frac{e^{-\lambda_b} \lambda_b^{Y_l}}{Y_l! (1 - e^{-\lambda_b})} \right\}$$

where $c_p(v)$ is the probability of capture history v for a given value of p . (For the removal setting of the previous example, $c_p(v) = (1-p)^{v^*} p^{l(v \neq 0)}$, where v^* is the number of non-captures (0's) before the first capture(1) in v .)

Now, collecting terms involving Y_l , cancelling the $(Y_l!)$ in the numerator and denominator, noting that the sum over Y_l can be expressed as the sum as $(Y_l - s_l)$ goes from 0 to infinity (the range of a Poisson random variable), the above equation can be greatly simplified to

$$P(A_l) \propto \sum_{b=1}^B u_b \exp \left(\lambda_b \left[\sum_{w=1}^W r_{bw} c_{p_{bw}}(0) \right] \right) \cdot \lambda_b^{s_l} \cdot \left[\pi \left\{ \sum_{v \neq 0} \sum_{w=1}^W r_{bw} c_{p_{bw}}(v) \right\} \right]^{k_l(v)} \cdot \left(\frac{e^{-\lambda_b}}{(1 - e^{-\lambda_b})} \right)$$

no longer involving Y_l .

Now,

$$P(A_{none}) = \sum_{b=1}^B u_b \sum_{Y_l=1}^{\infty} \left\{ \left[\sum_{w=1}^W r_{bw} c_{p_{bw}}(0) \right]^{Y_l} \cdot \frac{e^{-\lambda_b} \lambda_b^{Y_l}}{Y_l! (1 - e^{-\lambda_b})} \right\}.$$

Using properties of the Poisson density function, this can also be simplified to

$$P(A_{none}) = \sum_{b=1}^B u_b \left[\exp \left(\lambda_b \left[\sum_{w=1}^W r_{bw} c_{p_{bw}}(0) \right] \right) - 1 \right] \cdot \left[\frac{e^{-\lambda_b}}{(1 - e^{-\lambda_b})} \right],$$

not involving Y_l .

We utilized the nlminb (non-linear minimization with bounded constraints) procedure in Splus and the related optim procedure in R in order to find the maximum likelihood estimates of the parameters. Due to the complexity of the above likelihood, it was important to specify the derivatives within the procedures. Still, for some data sets and specifications of B and W, convergence could not be obtained. More convergence difficulties arose when t (the number of capture periods) was small, when B was large, or when the data often had very small numbers of observed individuals per species (i.e. small s_i 's). Submodels, e.g. forcing a common λ or forcing a common probability p of capture either within and/or between species, were also examined. Often some submodel was found to be the “most informative” model, see Section 3.2. Also, submodels had less convergence difficulties.

3.1.1 Removal Setting: Model M_{bh}

As illustrated in the motivating example of Section 2, our methodology and likelihood are appropriate in the removal setting, where animals are removed upon first capture. As stated above, for this setting, $c_p(v) = (1-p)^{v^*} p^{I(v \neq 0)}$.

3.1.2 Capture-recapture Setting: Model M_h

Our general methodology and likelihood are also appropriate for the capture-recapture setting where animals are not removed upon first capture but (are marked and) are available for capture on subsequent periods. In particular, for the capture-recapture setting M_h which allows heterogeneity (h) in capture probabilities among individuals, but does not allow time or trap effect, the above likelihood is appropriate with $c_p(v) = p^{j_v} (1-p)^{(t-j_v)}$, where j_v is the number of captures (1's) in v .

3.2 Submodels and Model Selection

Our full model allows heterogeneity in the species' Poisson parameters (the λ 's), heterogeneity in capture probabilities between species (the p_b 's), and heterogeneity in capture probabilities within species (the p_w 's). As mentioned in our motivating example of Section 2, sometimes a simpler model is more appropriate for a given situation. This might be due to apriori knowledge or due to applying model selection criteria to the study's data.

One general submodel excludes heterogeneity in the species' Poisson means and heterogeneity in capture probabilities between species. Its likelihood is a straightforward simplification of the full likelihood by just eliminating the "b" subscript (ie. having $B=1$). We label this submodel as "no λ h", short for no λ heterogeneity.

The second general submodel excludes heterogeneity in capture probabilities *within* species. Its likelihood is also a straightforward simplification of the full likelihood by just eliminating the "w" subscript (i.e. having $W=1$); this submodel is labeled "noph". A further simplification of this submodel forces the same capture probability p for each λ (i.e. for each b); this simplification is labeled "noph1p". The simplest model eliminates all (λ , p -within, and p -between) heterogeneities. Its likelihood eliminates the "b" and "w" subscripts from the full likelihood, i.e. has $B=1$ and $W=1$.

For a given setting and data set, we must "select" a model. In those models where either B or W is not restricted to be 1, we must also select an appropriate value for the non-restricted B or W . Apriori knowledge may eliminate some models; however, several potential models will probably remain. To test between two nested models, a bootstrap likelihood ratio test could theoretically be utilized, see, e.g. Norris and Pollock (1996). However, for the current paper, it

requires several minutes of computer time to obtain a single likelihood maximization; therefore a bootstrap test, say, requiring $2 \times 100 = 200$ maximizations, is burdensome. As a general model selection tool for our setting, we recommend the use of AIC. Although the regularity conditions for AIC are not met for some mixture model comparisons, Burnham and Anderson (2002) give support for using AIC for mixtures. AIC seems to give good discrimination between our models, especially since the AIC-adjusted log likelihoods of our models tend to substantially differ.

3.3 *Estimating standard deviations*

The hessian matrix of the maximized log likelihood can provide a rough asymptotic foundation for estimating the standard deviations of the mle estimates; however, the asymptotic regularity conditions are not met for our finite mixture models (see, e.g. Titterton (1991)). Our best estimates of the standard deviations would come from bootstrap standard deviation estimation, requiring, say 30 bootstrap replications (see, e.g. Efron (1981)); thus we utilize this bootstrap approach in our paper.

4. Ecological diversity and evenness measures

Ecological diversity and evenness measures have a very long history with numerous proposed measures and thousands of historical references. Fortunately, a few papers (principally, Patil and Talle (1979) and Rao (1982a, b)) have placed individual measures in a general framework and have thus greatly added to the theoretical foundations of ecological diversity and evenness. However, in practice, these methods have still been applied to *observed* abundances only, except for estimating N ; our paper allows these methods to be applied to *true* abundances. This is especially important since observance (capture) probabilities often differ between species. We

also develop a new “diversity in process means” measure which has interesting conceptual properties.

Patil and Taille (1979) showed that any diversity index can be viewed as an “average rarity”. For our model-based context with “ $R(\cdot)$ ” denoting the rarity function,

$$\text{Average Rarity} \equiv N \cdot \left(\sum_{j \geq 1} \left[R(\tau_j) \cdot \tau_j \cdot P_{j,F} \right] \right) ,$$

where $P_{j,F}$ denotes the probability that our zero-truncated Poisson(F) mixture of true abundances takes the value j , while

$$\tau_j \equiv \left(\frac{j}{N \cdot \sum_{j \geq 1} (j \cdot P_{j,F})} \right)$$

is the model-based (true) relative abundance of a given species having (true) abundance j . Our mle for τ_j and average rarity are obtained by simply substituting our mle’s for N and F into the above equations. The Shannon diversity index is simply an average rarity with $R(\tau_j) = -\log_e(\tau_j)$, while the Simpson diversity measure is an average rarity with $R(\tau_j) = 1 - \tau_j$ (see Shannon and Weaver (1949) and Simpson (1949) for original discussion of these two important indices). It should be emphasized that our method “automatically” adjusts for differences in capture probabilities since F is the portion of our model that (only) is associated with true abundances and not capture probabilities.

Rao (1982a, b) introduced the concept of the *average diversity coefficient* (adc). For individuals from a population, $\text{adc} = E(\text{DC}(i_1, i_2))$, where $\text{DC}(i_1, i_2)$ is an assigned diversity coefficient between two randomly selected individuals i_1 and i_2 . For $\text{DC}(i_1, i_2) \equiv I(i_1 \text{ and } i_2 \text{ are of different species})$, then the adc (for individuals) is simply the Simpson diversity. Later in this section, we propose an adc for the Poisson processes’ λ ’s.

Another interesting theoretical concept presented by Patil and Taillie (1979) is that of an *intrinsic diversity profile*, which provides a comprehensive examination of the differences in two regions' diversities. In particular, if the intrinsic diversity profile for one region is everywhere above that for the other region, then the former region is said to have intrinsically more diversity than the later. For our model-based profile, an (x_k, y_k) point of a profile has $x_k =$ [the expected total relative (true) abundance of all those species having abundance $\geq k$], and $y_k =$ [the expected number of species having abundance $\geq k$]. Thus, $x_k = 1 - N \cdot \sum_{j < k} (\tau_j \cdot P_{j,F})$ and $y_k = N \cdot (1 - \sum_{j < k} P_{j,F})$, which are simply estimated by substituting the mle's for N and F.

Many different *evenness* (of species' abundances) *measures* have been proposed to measure the "similarity in the abundances of the species, on a 0.0 to 1.0 scale". As with diversity measures, evenness measures have been based on observed abundances rather than having been based on true abundances. However, our method yields estimates of evenness based on true abundances. The Shannon evenness in abundance measure is probably the most popular one; for our setting, this measure is just our Shannon diversity measure divided by its largest possible value of $\log_e(N)$. Other existing evenness in abundance measures are also simply expressed as functions of N and F; their formulas correspond to the respective formulas shown in Norris and Pollock (1998), however, now our F is for true abundances rather than for observed abundances.

Earlier in this section, we examined the *average diversity coefficient* (adc) for individuals from the population. We now construct an adc for the Poisson processes' means (the λ 's). The adc of these means is $E(DC(\lambda_1, \lambda_2))$ where the two λ 's are independently chosen from F. If the diversity coefficient is relative squared error, i.e. $DC(\lambda_1, \lambda_2) = [(\lambda_1 - \lambda_2)^2 / \mu_F]$ then the adc for the λ 's is simply $2 \cdot (CV_F)^2$, where CV_F denotes the coefficient of variation of F. An important interpretation of this adc is as follows: if the adc for the λ 's is small, then all abundances

(although they may differ considerably) were generated from similar Poisson(λ) processes. In other tangentially-related capture-recapture/removal research, Lee and Chao (1994), Carothers (1979) and Cormack(1966) have also used the coefficient of variation as an important measure of heterogeneity.

5. Detailed Results on our Motivating Example and Test Data Sets

In this section, we present detailed results for our motivating fisheries example of Section 2. Table 1 presents the raw data for the May 2002 Lumbee River removal study of Section 2, while Table 2 presents its relative AIC values for each model and submodel up to $B=5$ and $W=2$; Pledger (2000) demonstrates that even considerable heterogeneity in p can often be modeled with only 2 points of support for p (i.e. $W=2$ in our setting). Based on AIC, the best model (smallest AIC) is the submodel with $B=4$ (λ 's) and $W=1$ (p per λ) with a common p for different λ 's (a *nopl* model). The mle's for the four λ 's are 2.60, 10.21, 37.72 and 99.46, with respective weights (u 's) of 0.289, 0.370, 0.211, and 0.130, thus predicting substantial heterogeneity in the λ 's. It is instructive to compare these mle's with the raw data (of Table 1). Note that about two-thirds of these species have less than 15 individuals each (the column totals); this corresponds to having total weight of 0.66 (0.29 + 0.37) on small λ values. Also, 3 of the 23 observed species had at least 65 individuals each, which corresponds to a weight of 0.13 on a large λ of 99.46.

For key summary measures, their mle's and corresponding bootstrap-generated standard deviations (placed in brackets) are as follows: for mean of F (i.e. mean of λ 's), 25.38 [5.98]; for CV of F , 1.23 [0.167]; for common p , 0.437 [0.0255]; and for N , 23.0 [0.487]. For diversity and evenness measures, their mle's and corresponding bootstrap-generated standard deviations are as

follows: for Simpson diversity, 0.889 [0.0159]; for Shannon diversity, 2.509 [0.109]; for Shannon evenness, 0.800 [0.0356]; and for our diversity in process means, 3.04 [0.749].

[Put Tables 1 and 2 about here.]

Dr. Kwak and his colleagues conducted four other real-life fish studies with three passes (removal periods) per study. Unfortunately, convergences were so poor for these data sets that we could not select appropriate models or make reasonable parameter estimates. Probably, the convergence difficulties were mainly due to only having $t=3$ capture periods. In the test data sets, below, we illustrate that few convergences difficulties tend to occur with moderate t , say $t \geq 5$.

We examined several test data sets which, by their construction, suggested particular models or submodels. This was done for both the capture-recapture setting and the removal setting. We examined three test data sets under the *capture-recapture* setting; each of these had $t=6$ capture periods. Convergences were obtained for almost all of the models and submodels for each of these test data sets; only 2 of the 3×14 runs did not converge. One of these capture-recapture test data sets, labeled *ctot.dat*, was constructed to be indicative of a setting with $B=3$ different λ 's and sizeable heterogeneity in capture probabilities both between and within species, $W=2$. For a capture-recapture illustration, we present details on the results for this data set. This data set is shown in Table 3 with its AIC results shown in Table 4. From Table 4, note that the AIC-selected model is, indeed, the $B=3$, $W=2$ model, with heterogeneity within species ($W=2$) being very important. For this model, the mle's for the λ 's, their weights (u 's), the two-dimensional p 's and their weights (r 's) are presented in Table 5. By comparing the data and

basic results (Tables 3 and 5), one can see that our results match well with what is suggested by the data. For example, the data suggest three (equal-sized) groups of species, with the last two groups having substantial heterogeneity of capture within species; also, the last group's capture probabilities appear to be larger than those of the other two groups. All of these data suggestions are realized in our results.

The mle's and corresponding bootstrap-generated standard deviations (placed in brackets) for key summary measures are as follows: for mean of F (i.e. mean of λ 's), 49.40 [8.503]; for CV of F, 0.330 [0.061]; for mean of p's, 0.346 [0.022]; and for N, 24.0 [0.0]. For diversity and evenness measures, their mle's and corresponding bootstrap-generated standard deviations are as follows: for Simpson diversity, 0.953 [0.002]; for Shannon diversity, 3.108 [0.020]; for Shannon evenness, 0.978 [0.006]; and for our diversity in process means, 0.217 [0.076].

[Put Tables 3, 4, and 5 about here.]

A second capture-recapture test data set, labeled *cnoph.dat* was constructed to be indicative of a setting with B=3 different λ 's and heterogeneity in capture probabilities between species but not within species (W=1). The best AIC model has B=3 and W=2, but having W=2 was not nearly as critical as it was with the *ctot.dat* data set. Also, allowing heterogeneity in capture probabilities between species (**not** allowing the *noph1p* nor *noph1* models) was found to be very important for this data set, as predicted. The last capture-recapture test data set, labeled *cnoph1p.dat* was constructed to be indicative of a setting with B=3, W=1 and a common (single) p over all λ (a *noph1p* model). The best AIC model has B=3 and W=2, but again having W=2

was not nearly as critical as it was with the *ctot.dat* data set. Although a full ($W=2$) model performed best, the *noph1p* models outperformed the *noph* models (based on AIC) suggesting that there might be no substantial heterogeneity in capture probabilities between species, as predicted.

Each of the removal test data sets involved $t=5$ capture periods, and for each, we obtained convergences on all models and submodels. One removal test data set, labeled *rtot.dat*, was constructed to be indicative of a setting with $B=3$ different λ 's and heterogeneity in capture probabilities both between species and within species, $W=2$. Our method performed well on this test with the $\{B=3, W=2\}$ model's AIC being at least 5.0 below that of any of the other models. Another removal test data set, labeled *rnoph.dat*, was constructed to be indicative of a setting with $B=3$ different λ 's and heterogeneity in capture probabilities between species but *no* substantial heterogeneity within species ($W=1$). Based on AIC, this target model was clearly the best for this data set, having AIC at least 6.0 below that of any other model. The last removal test data set, labeled *rnoph1p.dat*, was constructed to be indicative of a setting with $B=3$ different λ 's and *no* substantial heterogeneity between or within species. Again based on AIC, the target model was the best, having AIC at least 2.8 below that of any other model. Overall, our methods worked well on the test data sets.

6. Discussion

In this paper we develop a general multiple species model which yields inferences on true species abundances. This allows us to base existing diversity and evenness measures on true abundances rather than observed abundances. We also develop a new “diversity in process” measure which has important conceptual meaning. In addition, we are able to examine and

adjust for heterogeneity in capture probabilities both between and within species. We detail our methods on a motivating fisheries example, and we examine the utility of our methods on several test data sets from removal studies and from M_h capture-recapture studies.

We chose to take a finite mixture approach for handling heterogeneity in the capture probabilities and differences in the species' mean abundances. The nonparametric and flexible nature of the finite mixture approach, as well as its ability to differentiate unknown subgroups were especially appealing. Alternatively, an infinite, parametric mixture approach could have been utilized; comparison of its performance to our finite nonparametric approach could be a topic for further investigation. We also chose to use a maximum likelihood estimation approach rather than a Bayesian approach. Utilizing Bayesian methodology and associated Markov Chain Monte Carlo (MCMC) simulations would conceptually be fairly straightforward (although the simulations would be somewhat complex, possibly involving reversible jumps for model selection). However, in some of our settings, it may not be appropriate to assume independent priors between N , the process means, and the capture probabilities, making the specification of a "reasonable" prior much more difficult. In addition, especially when the number of capture probabilities or observed species is low, the Bayesian results may not be robust to other "reasonable" priors. It would be useful to explore prior specification and robustness through future research.

Currently, we are investigating the extension of our mle methods to other removal and capture-recapture settings. Some of these extensions are straightforward, such as with catch-effort models, which would just involve a new simple formula for $c_p(v)$, the conditional probability that an individual has capture history v , given that its chance of capture on a period of unit effort is p . Another extension could involve partitioning the target species into groups

which act independently, e.g. land birds and water birds; then our group-incorporated model's likelihood is simply the product of the likelihood (1) just for land birds and the likelihood (1) just for water birds. Extension of our methods to more general covariates and to the open population setting would be substantially more difficult and could be a topic for future research.

Our method assumes Poisson-based species abundances. Our model can be robust even over diverse areas since the sum of independent Poissons is Poisson; however, when individuals of a given species strongly attract or strongly repel one another (demonstrating strong lack of independence between individuals), then our Poisson model would not be reasonable. We are currently looking at extending our methods to account for these forces. Also, our model makes the simplifying assumption of independence between species. Different models should be considered when the species' abundances are thought to be highly dependent on one another, e.g. when multiple predator/prey pairs are within the set of target species.

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Table 1

Data for Lumbee river May 2002 study: Table entries are the numbers of individual animals with capture history v for each of the 23 observed species (each species results is a separate column).

$V=1$: 1 1 0 1 1 2 3 5 3 5 5 5 8 8 6 6 15 26 18 25 39 38 35
 $V=01$: 0 1 2 0 1 1 1 1 2 0 2 1 1 0 5 4 4 5 8 10 15 18 63
 $V=001$: 0 0 0 1 0 0 0 0 1 2 1 2 0 4 1 9 5 3 10 5 11 18 8

Table 2

Relative AIC values for each of the models and submodels for Lumbee river May 2002 data set.

	B=5	B=4	B=3	B=2	B=1
Full (W=2)	NC ²	NC	NC	NC	491.0
Noph W=1 no het within; het between	NC	2.0	6.6	76.6	NA ¹
Noph1p W=1 no het within; no het between	4.0	0.0	6.6	74.2	518.8

¹NA – not an applicable model, since for B=1, there is only one λ group.

²NC – non-convergence of maximizing algorithm.

Table 3

Raw data for the ctot test data set: Table entries are the numbers of individual animals being captured j_v times for each of the 24 observed species (each species results is a separate column).

$j_v=1:$	9	10	8	9	10	8	8	9	12	13	12	14	12	15	11	11	9	10	11	9	8	11	9	8
$j_v=2:$	5	6	5	4	5	5	4	5	7	6	5	6	5	6	7	5	15	14	17	16	14	17	16	17
$j_v=3:$	3	2	3	2	2	2	2	2	5	4	4	5	4	5	5	5	9	9	8	9	8	10	9	10
$j_v=4:$	2	1	1	2	1	1	2	3	11	10	10	11	9	12	10	11	8	7	6	5	7	10	7	8
$j_v=5:$	1	1	2	2	0	2	1	0	3	4	3	3	4	3	2	3	14	12	13	14	13	14	15	14
$j_v=6:$	0	1	0	0	0	0	1	0	1	1	1	2	1	2	3	1	3	4	3	5	3	4	3	4

Table 4

Relative AIC values for each of the models and submodels for ctot capture-recapture test data set

	B=5	B=4	B=3	B=2	B=1
Full (W=2)	20.0	10.0	0.0	48.6	159.6
Noph W=1 no het within; het between	345.4	339.4	333.4	367.0	NA
Noph1p W=1 no het within; no het between	455.2	451.2	447.4	456.2	555.8

Table 5

MLE's for the Poisson Means (λ 's), their weights (u 's), capture probability pairs ((p_1, p_2) 's), and weight of p_1 (r_1) under the best-fit ($B=3, W=2$) model for the ctot test data set

b	λ	u	(p_1, p_2)	r_1
1	26.4	0.33	(0.165, 0.634)	0.827
2	59.5	0.33	(0.085, 0.620)	0.611
3	62.3	0.33	(0.312, 0.777)	0.604