



Efficacy of depletion models for estimating abundance of endangered fishes in streams

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ABSTRACT

Conservation programs for imperiled fish require a sampling method for quantifying their habitat relationships and their progress toward recovery, via abundance estimation and subsequent monitoring. Depletion sampling is a commonly used method, although the assumptions of homogeneous capture probabilities are tenuous. Recently, Bayesian hierarchical models have been used to describe the conditional relationships between abundance of animals and detection probability, but their performance remains untested when detection varies across successive passes. We tested such approaches within a depletion-sampling framework for estimating abundance of three endemic and imperiled fish species in southeastern Arizona, USA. Our procedure uses depletion sampling, via simulation and field trials, and removes the untenable assumption of constant detectability across sampling passes. Specifically, we evaluated how population size, the number of depletion passes, the probability of fish detection, the amount of decline in this probability across removal passes, and the effects of variable detection probability affect bias and precision when using models with constant and variable detection probability. Abundance estimates were negatively biased when detection probability declined by 20% or more across successive passes, with detection probability < 0.30 on the first pass. When detection probability declined by < 10% across successive passes, unbiased estimates could be attained with detection probabilities of 0.20. Increasing depletion passes improved precision but not bias. Field trials underscored the importance of incorporating changes in detection probability among species and successive depletion passes. Our work demonstrates the efficacy of depletion experiments to estimate abundance, and highlights the importance of sampling a known abundance to accompany simulation analyses. Monitoring programs ignoring variability in detection probability using a depletion framework can produce biased abundance estimates.

1. Introduction

Conserving endemic and imperiled fish species requires measuring their recovery status and quantifying species-habitat relationships. Population abundance and trend data reveal their status, while species-habitat relationships steer management toward boosting population growth. Several sampling designs and modeling techniques exist for acquiring such data for lotic fish, but most ignore detectability (Schnute, 1983). Because detection probabilities are usually < 1.0, such procedures may bias abundance estimates and trends, while producing inaccurate species-habitat relationships (Nichols, 1986; Stewart et al., 2017a). We focus on depletion (i.e., removal) sampling, often used for estimating the abundance of demographically closed animal

populations (Seber, 1982). The method estimates initial abundance, and is adjusted by a detection rate for each sampling occasion (Dorazio et al., 2005). Particularly, it remains unknown if this procedure produces unbiased estimates of abundance unless methods that account for variable detection probability and overdispersion in animal abundance across sites are applied.

Historically, examining the effectiveness of depletion sampling relies on observational and experimental methods, with the former receiving most attention. For example, observational approaches typically draw comparisons between two survey techniques or different sets of model parameterizations (e.g., Edwards et al., 2003; Matson et al., 2018). Others have incorporated empirical analyses of long-term trends in population abundance, using various generalizations of abundance

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estimators, which form the focal point of the evaluation of the survey method (e.g., Roa-Ureta et al., 2015; Feenstra et al., 2017). In contrast to the observation approach toward survey evaluation, experimental approaches seek to exclude confounding effects using either a controlled or simulated condition (e.g., Hanks et al., 2018), and rely on manipulating conditions that may directly influence the capture probability of fish to evaluate the utility of the survey method (e.g., Habera et al., 2010). Neither approach is self-sufficient; disentangling the assumptions of depletion sampling and how this affects model-based estimates is needed to fully explore the utility of depletion sampling to index abundance of fish populations.

We embark on an experimental approach. Practically, we seek abundance, their population trends, and producing species-habitat information to recover three fish: Yaqui chub *Gila purpurea*, Yaqui topminnow *Poeciliopsis occidentalis sonoriensis*, and Mexican longfin dace *Agosia* sp. (USFWS, 1994; Miller et al., 2005). Analytically, we need assurance that depletion sampling produces accurate estimates. Therefore, this work centers on understanding and improving the utility of depletion models to estimate abundance and detection probabilities for spatially-distinct subpopulations of endangered small-bodied fish.

Depletion models for experimental data are based on four assumptions: (1) all animals have the same probability of capture, (2) the probability of capture does not change from one sample to the next (i.e., remains constant), (3) all removals from the population are known, and (4) the population is closed to any unknown changes (i.e., births, deaths, or migration) other than the known removals (Raleigh and Short, 1981; Williams et al., 2002). Adhering to these assumptions – that detection is constant over successive passes and the same for all animals and individuals – is risky. Heterogeneity arises from species, sex, age, size, individual variation, intensity of sampling, or sampling duration (Farnsworth et al., 2002; Peterson et al., 2004). Heterogeneity in detection probability must be accounted for if it is too great.

To address heterogeneous detection probabilities, both practical and statistical considerations have guided novel sampling designs. Procedures such as maintaining closed populations, reducing survey duration, using identical collection methods, and standardizing effort during each removal step, are believed to maintain the sampling assumptions and reduce heterogeneity in detection probability (Raleigh and Short, 1981). Alternatively, practitioners can use statistical models incorporating different detection probabilities for each subsequent removal occasion, while borrowing information from other subpopulations by estimating spatially-distinct detection probability and abundance parameter estimates (Dorazio et al., 2005). Previously, biologists recognizing this issue built models to incorporate declines in detection probabilities over successive passes (e.g., Schnute, 1983), and we consider these models. However, the degree that these procedures and detection models produce unbiased abundance estimates remains untested with actual removal data (Peterson et al., 2004).

We used simulation to test the hypothesis that bias and precision will be affected by population size, number of passes, and declining detection probability across passes. This hypothesis allowed us to evaluate how bias and precision in abundance were affected by

population size (low to high), the number of depletion passes, fish detection, the amount of decline in fish detection across removal passes, and the effects of variable detection when using constant and variable detection probability models. We then field tested the assumptions of these model-based simulations by establishing known population sizes of fish in their natural environments, and used depletion sampling with alternative model structures to estimate those known abundances. Since previous statistical approaches used simplified assumptions to account for stochastic sources of variation in the abundance parameter among subpopulations, we present an alternative to account for extra-Poisson variation (i.e., overdispersion) in simulations and field data. Our procedure provides the first unbiased abundance estimates for populations of these fish in lotic environments, establishes methods for monitoring population status, enables measuring recovery, and identifies species habitat preferences. We also improve the design of depletion models, while showing, empirically, the importance of incorporating detection heterogeneity for avoiding biased results, and identifying specific circumstances when this sampling method fails.

2. Methods

2.1. The model

We use a hierarchical Bayesian approach for fitting alternative formulations of depletion models. These models provide a natural way to incorporate alternative structures, such as latent variables for modeling, data augmentation, and inferences related to shape and scale, representing the uncertainty in the posterior probability distribution of the model parameters (Gelman, 2006). In general, hierarchical Bayesian models are adaptable to various capture-recapture experiments (in both marked and unmarked methods), such as depletion models that estimate abundance from unmarked individuals. The depletion survey is designed such that animals are captured from I spatially distinct sites on J different sampling occasions, and populations are demographically closed to changes in abundance, births, deaths, immigration, or emigration at the time of sampling (Table 1).

We consider the observed elements of the model to consist of the sequence of counts of unmarked individuals, y , from each sampling occasion $j = 1, \dots, J$ within each set of $i = 1, \dots, I$ sites. Therefore, the observed data, y_{ij} , can be denoted by the matrix of observed numbers of animals during the survey as $Y = \{y_{ij}; i = 1, 2, \dots, I; j = 1, \dots, J\}$ and is regarded as a binomial outcome $h(y_{ij}|N_{ij}, q_{ij})$ (or multinomial; Dorazio et al., 2005), as

$$L(q, \lambda; \{y_{ij}\}) = \prod_{i=1}^I \left\{ \sum_{N_i=\max y_{ij}}^{\infty} \left(\prod_{j=1}^J \text{Bin}(y_{ij}; N_i, q) \right) f(N_i; \lambda) \right\}$$

The outcome is conditional on the unknown total number of individuals available for sampling, N_{ij} , within site i , where the infinite summation is replaced over N_i by the summation of observations across passes at a site. Depletion surveys require the removal of captured individuals during occasion j . Under this specification, q_{ij} is defined as the

Table 1
Parameters used to define prior distributions for the hierarchical Bayesian depletion models with constant and variable detection models.

Effect	Equation	Parameter	Prior distribution	Prior parameters
Simulation analyses				
Fixed	$\log(\lambda_i) = \alpha$	α	$\alpha \sim N(\mu, \sigma^2)$	$\mu = 0$ $\sigma \sim \text{Unif}(0,10)$
Random	$N_i \lambda_i, \epsilon_i \sim \text{Pois}(\lambda_i \epsilon_i)$	ϵ_i	$\epsilon_i \sim \text{Gamma}(\phi \sim \text{Unif}(b, c), \phi \sim \text{Unif}(b, c))$	$b = 0$ $c = 100$
Random (Constant)	$y_{ij} q_i, N_{ij} \sim \text{Bin}(q_i, N_{ij})$	q_i	$q_i \sim \text{Beta}(d, e)$	$d = 1.1$ $e = 1.1$
Fixed (Variable m1)	$y_{ij} q_{ij}, N_{ij} \sim \text{Bin}(q_{ij}, N_{ij})$	q_{ij}	$q_{ij} = p_1 \sim \text{Beta}(d, e) +$ $(p_2 \sim \text{Beta}(d, e) - p_1 \sim \text{Beta}(d, e)) \times (1 - c \sim \text{Beta}(d, e))^{j-1}$	$d = 1.1$ $e = 1.1$
Fixed (Variable m2)	$y_{ij} q_{ij}, N_{ij} \sim \text{Bin}(q_{ij}, N_{ij})$	q_{ij}	$q_{ij} = p_1 \sim \text{Beta}(d, e)(1 - p_0 \sim \text{Beta}(d, e))^{j-1}$	$d = 1.1$ $e = 1.1$

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