

Estimating abundance without recaptures of marked pallid sturgeon in the Mississippi River

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## Abstract

Abundance estimates are essential for estimating the viability of populations and the risks posed by alternative management actions. An effort to estimate abundance via a repeated mark-recapture experiment may fail to recapture marked individuals. We present a framework for obtaining lower bounds on abundance in the absence of recaptures for both panmictic and spatially-structured populations. We applied this nil-recapture method to data from a 12-year survey of pallid sturgeon (*Scaphirhynchus albus*) in the lower and middle Mississippi River; none of the 241 individuals marked were recaptured in the survey. After accounting for survival and movement, our model-averaged estimate of the total abundance of age 3+ pallid sturgeon in the study area had a 1%, 5%, or 25% chance of being less than 4,600, 7,000, or 15,000, respectively. If we assumed fish were distributed in proportion to survey catch-per-unit-effort, then the furthest downstream reach in the survey hosted at least 4.5-15 fish per river kilometer (rkm), whereas the remainder of the reaches in the lower and middle Mississippi River hosted at least 2.6-8.5 fish  $\text{rkm}^{-1}$  for all model variations examined. The lower Mississippi River had an average density of at least 3.0-9.8 age-3+ pallid sturgeon  $\text{rkm}^{-1}$ . The choice of Bayesian prior was the largest source of uncertainty considered in this study, but did not alter the order of magnitude of lower bounds. Nil-recapture estimates of abundance are highly uncertain and require careful communication but can deliver insights from experiments that might otherwise be considered a failure.

## Introduction

Understanding, in absolute terms, the risks facing populations of concern requires an estimate of abundance (Ferson & Burgman 2000; Morris & Doak 2002; Williams et al. 2002). As with most of the information we need to know about rare species, an abundance estimate

may be elusive. For instance, a mark-recapture experiment may fail to yield recaptures. We demonstrate that lower bounds on abundance can be inferred even when no marked individuals are recaptured.

Intuitively, a mark-recapture experiment without recaptures could be remedied simply by continuing to sample. Though possibly impractical, this solution usefully casts recaptures as a rare event that has not yet been observed. The need to estimate the probability of events that have not yet occurred is far from novel and is, in fact, widespread. For engineers deploying new equipment, it is the risk of failures such as oil spills. For a doctor, it is the risk of adverse outcomes from a novel treatment. The probability of such events is seldom zero. By assuming that additional data collection would eventually yield an observation of interest, the number of non-detects becomes information (Louis 1981; Hanley & Lippman-Hand 1983; Jovanovic & Levy 1997; Smith & Winkler 1999; Andow et al. 2000; Winkler et al. 2002).

Naively, the absence of recaptures suggests that the focal population is very large, since the probability of recapture declines to zero as abundance approaches infinity. Yet, zero recapture is also likely whenever the effort required per capture is high, as might be true for organisms that are rare, have large home ranges, are cryptic, or live in environments that are difficult to sample. The problem is exacerbated by any factors that reduce the population of marked individuals, including mortality, emigration, or the loss of marks. If the fraction of marked individuals is low enough, the time between recaptures approaches or exceeds the scope of the study. It is then conservative to assume that the probability of recapture was high enough that a small number of recaptures were expected but were missed by random chance.

Attribution of zero recaptures to sampling error is compatible with the logic behind mark-recapture estimation methods. Such an approach was briefly set forth for two-sample studies of closed populations under the moniker “nil-recapture” estimation (Bell 1974), and further clarified as being limited to finding lower bounds on abundance (Edwards 1974). To our knowledge, the approach has only been used in a single published study (Bell 1977).

This study expands the method of nil-recapture abundance estimation to repeated mark-recapture experiments (Schnabel 1938) in spatially-structured populations. The use of Bayesian methods improves upon the interpretation of results, as well, by providing the probability that actual abundance exceeds a lower bound. We demonstrate the use of the method and its sensitivities to assumptions with a case study of the endangered pallid sturgeon, *Scaphirhynchus albus*, in the lower and middle Mississippi River in the United States. The resulting estimates, though highly imprecise, provide guidance on the lower bounds of abundance over a large portion of the species’ range despite the absence of recaptures over a twelve-year period of study (Hoover et al. 2007; Killgore et al. 2007a; Killgore et al. 2007b).

## Methods

For nil-recapture estimation of a closed population, Bell (1974) used the hypergeometric distribution, which accounts for sampling without replacement. In practice, a Poisson distribution will give similar answers so long as only a small fraction of the population is marked. The Poisson is easy to work with and permits the use of the familiar Schnabel estimator (Schnabel 1938; Chapman 1952).

## Data

Consider an experiment in which individuals are captured, marked, and returned to their environment on multiple sampling occasions. Let  $\mathbf{t}$  be a vector of the times (e.g., dates) at which each sample was collected. Sampling can be spatially structured. Let  $\mathbf{C}$  be a matrix containing entries  $c_{ij}$ , the record of captures on each occasion  $i$  in each spatial unit  $j$ . The total number of sampling dates is  $I$  and the number of spatial units is  $J$ . Finally, let  $R$  be the sum of all recaptures;  $R = 0$  in the nil-recapture situation.

## Abundance

Let  $N$  be the estimate of total population size over all spatial units and  $N_j$  the estimate for spatial unit  $j$ . We assume the  $N_j$  are fixed. Unless population changes are likely to make the population small, the assumption of constant abundance gives a rough estimate of abundance (Chapman 1954) and simplifies calculations.

We assume the marked population changes over time. Let  $\mathbf{M}$  be a matrix of projected numbers of marked individuals present on each occasion in each spatial unit,  $m_{ij}$ . We account for mortality (Chapman 1954), dispersal among spatial units (Hilborn 1990), and emigration (Williams et al. 2002). Calculation of each of these processes to obtain  $\mathbf{M}$  is described in the Case Study section below. Our assumption of a fixed population size implies a birth-death-immigration-emigration equilibrium.

## Spatial Structure

The nil-recapture estimate of abundance is driven by the number of individuals captured. When studying multiple spatial units, variation in the number of individuals captured in each unit may reflect actual differences in abundance or may be the result of variation in effort or catchability. The contribution of each spatial unit to the estimate of total abundance can be controlled through an assumption about the spatial structure of abundance. This constraint could be based, for instance, on a distribution model or catch per unit effort (CPUE) during the study (Williams et al. 2002; Killgore et al. 2007a). We express the constraint as a vector  $\mathbf{a}$  in which  $a_j$  is the proportion of the total population that resides in spatial unit  $j$ .

### Inference

Schnabel (1938) pointed out that the total number of recaptures expected is the sum of the expectations on each of the  $I$  sampling occasions because the distribution of the sum of independent Poisson distributions is itself Poisson. That is,  $E(R) = \frac{1}{N} \sum_{i=1}^I c_i m_i$ , where  $E$  indicates the expectation. By extension, if an experiment takes place in multiple spatial units then  $E(R)$  is the sum of expected recaptures in each unit. If  $N a_j$  individuals reside in unit  $j$ ,

$$E(R) = \frac{1}{N} \sum_{j=1}^J \left( \frac{1}{a_j} \sum_{i=1}^I c_{ij} m_{ij} \right). \quad \text{Eq. 1}$$

The Poisson probability of no recaptures is then

$$\Pr(R = 0 | N, \mathbf{a}, \mathbf{C}, \mathbf{M}) = e^{-E(R)}. \quad \text{Eq. 2}$$

Eq. 1 can be rearranged to describe the Poisson rate of recaptures per sampling intensity, where sampling intensity is the number of captures weighted by the size of the marked population and the presumed relative sizes of subpopulations, such that

$$\frac{1}{N} = E(R) \left[ \sum_{j=1}^J \left( \frac{1}{a_j} \sum_{i=1}^I c_{ij} m_{ij} \right) \right]^{-1} \quad \text{Eq. 3}$$

If recaptures occur randomly at rate  $1/N$ , then the waiting time, in terms of sampling intensity, has mean  $N$  (See Supplemental Material for more detail on Eq. 1 and a demonstration that the rate in Eq. 3 is constant with respect to sampling intensity).

In finding lower bounds, it would be useful to be able to make the statement that abundance is greater than  $N$  with some level of confidence. Bayesian credible limits allow this interpretation (Jaynes 1976). Given that the right side of Eq. 3 is a Poisson rate, the lower Bayesian credible limit can be obtained using a gamma conjugate prior (Bernardo & Smith 1994; Kerman 2011). Let  $\alpha_0$  and  $\beta_0$  define the prior gamma distribution using the rate parameterization. After accounting for observations, the posterior distribution has mean  $\alpha/\beta$  with  $\alpha = \alpha_0 + R$  and  $\beta = \beta_0 + \sum_{j=1}^J \left( \frac{1}{a_j} \sum_{i=1}^I c_{ij} m_{ij} \right)$ . Lower bounds on  $N$  as a function of possible expected recaptures ( $x$ ) can be found directly from the posterior Gamma distribution or from the  $\chi^2$  or exponential distributions. Using  $\chi^2$ ,

$$\Pr(N > \beta/x) = \chi^2[2x, \text{df} = 2(\alpha_0 + R)]. \quad \text{Eq. 4}$$

Estimates of  $N$  for particular levels of confidence can be then obtained with the  $\chi^2$  quantile function. In this study, we chose to focus on the 99%, 95%, and 75% one-tailed lower credible limits on abundance (examples in Supplemental Material). Eq. 4 can also be used to find the probability that abundance exceeds a given management threshold.

For reference, we also present frequentist and likelihood lower confidence limits, though these do not describe the probability of abundance (Neyman 1937). The frequentist lower bound on  $N$  in Eq. 1 with no recaptures is found from the upper confidence limit for  $E(R)$  (Garwood 1936):

$$\Pr(E(R) < x) = \chi^2(2x, df = 2). \quad \text{Eq. 5}$$

The likelihood approach leverages the approximately  $\chi^2$  distribution of relative likelihoods (Wilks 1938; Hudson 1971). Using Eq.2 as the likelihood function, the maximum likelihood is  $L = 1$  for  $N = \infty$ . The log relative likelihood of  $x$  recaptures is then  $\ln(e^{-x}/1) = -x$  and the upper bounds on  $E(R)$  can be found from

$$\Pr(E(R) < x) = \chi^2(2x, df = 1). \quad \text{Eq. 6}$$

The inequality on the left hand side of Eqs. 5 and 6 is algebraically equivalent to that in Eq. 4 if  $\beta_0 = 0$ . Two convenient gamma priors with  $\beta_0 = 0$  are the uniform ( $\alpha_0 = 1, \beta_0 = 0$ ) and the Jeffreys ( $\alpha_0 = 0.5, \beta_0 = 0$ ) (Gelman 2006). Substituting these priors into Eq. 4, the uniform produces the same the lower bound as the frequentist confidence limit (Eq. 5), while the Jeffreys reproduces that found from the likelihood confidence limit (Eq. 6). Many other priors are possible, of course. With no recapture data to overwhelm the  $\alpha_0$  hyperparameter, the choice of prior can strongly affect inferences on the lower bounds of abundance. This sensitivity is a recognized characteristic of Bayesian inference for rare or unobserved events (Winkler et al. 2002; Gelman 2006; Kerman 2011; Webster & Kemp 2013) and was our motivation for using priors that reproduce the answers obtained using non-Bayesian approaches.

### Case Study

The pallid sturgeon, *Scaphirhynchus albus*, was listed as endangered in 1990 (55 Federal Register 36641-36647) with presumed low population sizes and recruitment due to overfishing, habitat modifications, pollution, and hybridization (Dryer & Sandvol 1993). The



range of the pallid sturgeon includes the Missouri River as well as the middle Mississippi River (MMR), between the mouths of the Missouri and Ohio Rivers, and the lower Mississippi River (LMR). Pallid sturgeon do not occupy the upper Mississippi River due to impoundment and are thought to be rare or absent below New Orleans (Dryer & Sandvol 1993). Pallid sturgeon may have once been common in the MMR. The LMR population was poorly documented and thought to be sparse (Duffy et al. 1996). However, the abundance of pallid sturgeon relative to its sister species, *S. platorhynchus*, has long been observed to increase downstream (Forbes & Richardson 1905; Bailey & Cross 1954; Killgore et al. 2007a).

A long-term survey effort in the Mississippi River captured and marked hundreds of individuals between New Orleans, LA, and the mouth of the Missouri River (Hoover et al. 2007; Killgore et al. 2007a; Killgore et al. 2007b). None of the marked individuals was recaptured in the Mississippi River (Killgore et al. 2007a).

A thorough explanation of the survey, study area, and reach delineations can be found in Killgore et al. (2007a). Briefly, the survey dataset covered 12 years (1997-2008). The river was divided into reaches characterized by geomorphology and river management for navigation and flood control. Reach A, the 153 river kilometers (rkm) of river south of New Orleans, yielded no pallid sturgeon and was not considered in this study. Reach B extended 349 rkm from New Orleans to the mouth of the Atchafalaya River. Reach C included the next 433 rkm to the mouth of the Arkansas River. Reach D extended the next 598 rkm to the mouth of the Ohio River, the northern limit of the LMR. The northernmost reach comprised the 314 rkm of the MMR to the mouth of the Missouri River. (The survey divided the MMR into two reaches, E and F, that are here combined.)

Sampling locations were largely driven by access. The allocation of effort across reaches changed over time with the greatest total effort expended in the first half of the survey. All sampling bouts used trotlines in a consistent manner throughout the study period. Each trotline was 61 m long, with 60 hooks baited with worms, and was deployed for approximately 16 h from late afternoon until the following morning. Each sampling event in the survey consisted of up to 8 trotlines. Captured fish were marked with a numbered Floy tag along the base of the dorsal fin. In addition, pallid sturgeon that did not already have an internal passive integrated transponder tag were injected with one. Given the use of two tags, tag loss was considered negligible. Floy tag retention has been demonstrated in the MMR (Hintz et al. 2016).

The youngest individual captured during the survey was three years old (Killgore et al. 2007b). We therefore assumed our abundance estimate reflects only that proportion of the population that is age-3+.

We sought estimates of abundance in each of the river reaches, requiring constraints on spatial structure. Two sets of constraints were investigated. The first assumed uniform population density along the length of the survey area. This structure places 21%, 26%, 35%, and 19% of the population in reach B through the MMR, respectively. The second assumed that spatial variation in population density was described by the reach-specific catch per unit effort (CPUE) observed during the survey, placing 33%, 19%, 33%, and 15% of the population in reach B through the MMR, respectively. We explored two spatial structures because it was not clear whether CPUE measured relative abundance, detectability, or the degree of aggregation at sampling locations.

## Estimating marked individuals

To populate the matrix,  $\mathbf{M}$ , we projected the number of marked fish in each reach on each sampling date. We assumed population size was at a constant birth-death-immigration-emigration equilibrium, but the number of marked fish could grow with new captures or decline with mortality.

The matrix  $\mathbf{T}$  projects daily changes in the marked population attributable to dispersal ( $d$ ), survival ( $s$ ), and fidelity to the river ( $v$ ),

$$\mathbf{T} = \begin{pmatrix} s_1 v (1 - d_1) & s_1 v d_1 & & & \\ s_2 v d_2 & s_2 v (1 - 2d_2) & s_2 v d_2 & & \\ & s_3 v d_3 & s_3 v (1 - 2d_3) & s_3 v d_3 & \\ & & s_4 v d_4 & s_4 v (1 - d_4) & \end{pmatrix}, \quad \text{Eq. 7}$$

where subscripts refer to the four reaches modeled. The marked population extant on sampling occasion  $i$  is given by the row vector  $\mathbf{M}_i = (\mathbf{M}_{i-1} + \mathbf{C}_{i-1})\mathbf{T}^{t_i - t_{i-1}}$ .

We assumed that survival, emigration, and population size remained constant over the survey period, tagging did not affect survival or detectability, tags were not lost, and populations were well-mixed within reaches.

Daily mortality and emigration were modeled deterministically, resulting in fractions of marked fish. Annual survival of pallid sturgeon in the LMR has been estimated to be 0.93 for detectable age classes (Killgore et al. 2007b). This survival rate was used in a previous population model (Bajer & Wildhaber 2007) and is near the rate measured in the lower Missouri River (Steffensen et al. 2010). Survival in the MMR was set lower, at 0.70 per year (Killgore et al. 2007b), to reflect that the survey was conducted before the moratorium on

commercial fishing for *S. platorhynchus* there, which impacted pallid sturgeon through the species' similarity of appearance. For an alternate panmictic model, we averaged reach-specific survival rates, weighting by reach length, to obtain a river-wide survival of 0.887. Additional loss of marked individuals arose from the assumption of emigration out of the study area. Our baseline model assumed 10% of fish emigrated annually and never returned. Sensitivity to the emigration rate was tested by evaluating abundance with 0% and 20% emigration, as well.

Movement between reaches was assumed to be balanced such that it did not alter the spatial structure of abundance. Observations of pallid sturgeon movement include individuals with high site fidelity (Bramblett & White 2001) as well as dramatic, long distance relocations (Mayden & Kuhajda 1997; Killgore et al. 2007a). In a telemetry study in the MMR (Koch et al. 2012), 7 of 84 tagged pallid sturgeon dispersed out of the reach in a year, suggesting an annual dispersal rate of 0.083 with a 95% confidence interval of (0.024, 0.143). We explored two levels of dispersal rates enclosing the 95% confidence interval for exchange between neighboring reaches: no dispersal and 15% annual dispersal from the MMR to reach D.

Dispersal from each reach,  $d_j$ , was set by assuming that net emigration and immigration from the system is balanced and the birth rate is the same in all reaches. Further, we assumed that dispersal compensates for differences in relative survival among reaches such that there is no change in spatial structure over time. We assumed that dispersers from the central reaches, C and D, move both upstream and downstream, while those in the extreme reaches, B and the MMR, move only toward the central reaches. In one time step, dispersal only connects adjacent reaches. All dynamics were modeled with a daily time step assuming 365 days per year. Hence, survival,  $s_i$ , was  $0.7^{(1/365)}$  in the MMR and

$0.93^{(1/365)}$  elsewhere, dispersal from the MMR,  $d_4$ , was  $1 - 0.85^{(1/365)}$ , and fidelity to the Mississippi River,  $v$ , was  $0.9^{(1/365)}$ .

Dispersal estimates depended on spatial structure. With relative survival per reach  $\lambda_j = s_j / \sum a_j s_j$ , the dynamics of the MMR can be described as  $a_{4,t+1} = a_4 \lambda_4 (1 - d_4) + a_3 \lambda_3 d_3$ . Setting  $a_{4,t+1} = a_4$ , the dispersal rate from reach D is  $d_3 = [a_4 - a_4 \lambda_4 (1 - d_4)] / a_3 \lambda_3$ . For reaches C and B,  $d_j = [a_{j+1} - a_{j+1} \lambda_{j+1} (1 - d_{j+1}) - \lambda_{j+2} d_{j+2}] / a_j \lambda_j$ . These formulas were evaluated sequentially starting with the estimate of  $d_4$  for the MMR and working southward.

## Results

### Marked Individuals

In total, 50, 64, 70, and 57 pallid sturgeon were caught and marked in reaches B, C, D, and the MMR, respectively, from 1997 through 2008. The maximum number caught on a sampling occasion was 10 individuals and the median was 2 (Killgore et al. 2007a). The number of marked fish in each reach, projected without dispersal, peaked during the middle years of the study (Fig. 1).

The probability of dispersing was highest in reach C and differed the most between spatial structures in reach B (Table 1). Annual inter-reach movement rates were high. Dispersal introduced marked fish to the MMR earlier in the study, before the first fish was marked there in 2002. This in turn increased exposure to the MMR's elevated mortality rate, reducing the total number of marked fish projected to exist at the end of the study, from 78

(no dispersal) to 72 (uniform) and 73 (CPUE). The panmictic model projected a final total of 76 marked individuals.

### **Pallid Sturgeon Abundance**

The largest source of uncertainty investigated in this study came from the choice of prior for Eq. 3. The Jeffreys prior produced a less rapid decline in support for larger population sizes than did the uniform (Fig. 2), resulting in bounds on abundance that were higher and varied more between credible limits. Averaged over model variations, lower bounds obtained through the use of the Jeffreys prior were 137%, 157%, and 213% higher than those for the uniform prior at the 99%, 95%, and 75% credible limits, respectively. The average probability that there are more than 5,000 age 3+ pallid sturgeon in the Mississippi River was 0.984 and 0.996 with the uniform and Jeffreys prior, respectively. The remainder of the results only report bounds found using the uniform prior because they are more conservative.

Lower bounds were relatively robust to assumptions made about spatial structure and dispersal (Table 2). The CPUE-based estimate was approximately 10% higher than that gained from the uniform density, which was, in turn, approximately 6% higher than the panmictic model. Limited dispersal between neighboring reaches increased uniform abundance estimates by 6% and CPUE abundance estimates by 5%. The three credible limits evaluated provided a range of lower bounds on total abundance from roughly 4,100 to 17,000 age 3+ fish across models (Table 2).

Lower bounds on abundance were also sensitive to the emigration rate used to project the number of marked individuals. Evidence for emigration comes from the recapture of one marked fish reported by a commercial fisherman in the Obion River, TN (Killgore et al.

2007a). Baseline models conservatively assumed a 10% annual rate of emigration. A doubling of annual emigration to 20% decreased lower bounds an average of 16% (Table 3). Decreasing emigration to 0% increased estimates 18% (Table 3). Sensitivity to annual survival would be identical.

Spatial constraints directly affected reach-level abundance estimates (Fig. 3). The uniform model, with 21% of the total population in reach B, yielded a lower 95% (99%-75%) bound on local abundance of 1,500 (900-3,000) age 3+ fish without dispersal (Fig. 3b). In contrast, the CPUE model placed 33% of the population in reach B, with a lower bound on abundance of 2,400 (1,600-5,200) age 3+ fish (Fig. 3b) without dispersal. The panmictic and uniform spatial models produced similar lower bounds on river-wide population density of 3.7 (2.4-8.0) and 3.9 (2.6-8.5) age 3+ fish  $\text{rkm}^{-1}$ , respectively (Fig. 3a). The CPUE model suggested a higher density in reach B of 6.5 (3.8-18.9)  $\text{rkm}^{-1}$ , making its estimate of total LMR density higher than that of the MMR, with 4.5 (3.0-9.8)  $\text{rkm}^{-1}$  versus 3.6 (2.3-7.8) age 3+ fish  $\text{rkm}^{-1}$ , respectively.

## Discussion

The ability to extract information from a mark-recapture experiment without recaptures can provide key supporting information for the assessment and management of rare or difficult-to-detect species. Our case study of pallid sturgeon in the lower and middle Mississippi River provides an example of the application of nil-recapture abundance estimation and gives insights into how this information might inform management decisions.

The nil-recapture framework relies on a simple concept, that the absence of recaptures is consistent with the sampling error associated with recapture probability. Taking a Bayesian approach allows the user to make a statement about the probability that abundance exceeds a given lower bound. Presenting lower-bound information effectively may require care. Reporting that the average of our models suggested that the Mississippi River between New Orleans and the mouth of the Missouri River contains at least 4,600-15,000 age 3+ pallid sturgeon may be interpreted as a confidence interval around the true mean. The correct interpretation is that it is 25 times more likely that abundance exceeds the lowest bound than the highest bound. It may also be confusing to compare lower bounds to estimates of mean abundance from other studies. For instance, a mark-recapture experiment in the MMR recently estimated a population of roughly 1,500 pallid sturgeon (Hintz et al. 2016), slightly above our 95% lower bound of 1,200-1,300 age 3+ fish and likely to address similar age classes. A prior range-wide estimate of 6,000-21,000 individuals (Duffy et al. 1996) overlaps the 95% lower bound on population density in our study, though it is not clear what age classes were included in the wider estimate. Wild pallid sturgeon in one reach of the lower Missouri River occur at a density of 5.4-8.9 fish  $\text{rkm}^{-1}$  (Steffensen et al. 2012), in line with our lower bounds for the uniform Mississippi River population density of 2.6-8.5 age 3+ fish  $\text{rkm}^{-1}$ . Presenting a series of such comparisons is likely to encourage the interpretation of lower bounds as estimates of the mean, but is necessary to evaluate whether the lower bounds appear reasonable.

We found that nil-recapture estimates are highly sensitive to the choice of prior. Two standard non-informative priors we investigated, the uniform and the Jeffreys, yielded lower bounds on abundance that were more than 100% different. While this sensitivity introduces an element of subjectivity into the estimation framework, an examination of Figure 2 shows



that the probability of exceeding low abundance thresholds was similar between priors, suggesting that the method can contribute substantively to conservation assessments. For instance, the two priors gave greater than a 98% chance that the population was larger than 5,000 age 3+ individuals. The nil-recapture focus on lower bounds may also be useful when the number of recaptures is very small, as the central estimate can be biased in such cases (Chapman 1952).

While lower bounds on total abundance were also very sensitive to survival and emigration, they were only moderately sensitive to uncertainty about spatial structure, suggesting that users can safely make simplifying assumptions like uniform population density. The spatial constraints did affect the distribution of abundance among reaches. Assuming CPUE indicated relative abundance, a large proportion of the population was estimated to reside in Reach B, which lacks hard substrates (Baker et al. 1991) that are thought to serve as spawning habitat (Dryer & Sandvol 1993). This would place more importance on Reaches C and D of the LMR, which may comprise the best remaining habitat in the pallid sturgeon range due to their relatively low channelization and absence of impoundments or major diversions (Baker et al. 1991). These reaches may act as sources for populations both upstream and down. There is evidence from body condition that adults in the LMR make upstream spawning migrations (Hoover et al. 2007) and large seasonal movements have been observed in other parts of the range (Bramblett & White 2001; Koch et al. 2012). Insight into inter-reach and age-specific habitat use could affect nil-recapture estimates through modification of the models used to project the number of marked individuals present during sampling.

The lack of recaptures in the Mississippi River survey is perhaps not very surprising, given the small number of marked fish that existed at any given time over the study period

and the large size of the study system. Reduced sampling effort and projected attrition led to declines in the projected marked population in the latter part of the study, further reducing the chances of a recapture. If sampling had been more intense but still failed to recapture any individuals, the lower bounds on abundance would be greater.

In our focus on introducing the nil-recapture method, we neglected several potentially important influences on the abundance estimate. Individual heterogeneity in capture probability attributable to factors such as age or size can lead to a significant negative bias (Otis et al. 1978; Chao et al. 1992). That younger age classes were rare among captures (Killgore et al. 2007b) suggests the presence of such bias. Also, a relaxation of the assumption of constant population size to explore the effects of population trends or environmental variability would increase the relevance to management. Likewise, projections could include the loss of marks or low matchability. The nil-recapture concept is compatible with approaches that include both greater biological realism and uncertainty quantification, allowing a fully Bayesian framework if desired.

Ultimately, lower-bounds serve a specific purpose, answering the one-tailed question of how small a population might be. This answer can be useful for assessing population status and provides an objective input for analyses aimed at quantifying worst-case impacts of management. For instance, it allows the conversion of a raw number of individuals impacted by some source of mortality, such as bycatch (Bettoli et al. 2009), into a per capita rate. As with other risk-based status assessments, the onus is on decision-makers to select a probability threshold upon which to base actions.

Lower bounds can be useful for comparisons between populations that are well-characterized and those that are less so. For instance, the population of hatchery-raised

pallid sturgeon in the lower Missouri River is known to be considerably more dense than that of wild individuals (28.6-32.3 adult fish per rkm Steffensen et al. 2012) and is spreading into the Mississippi River (Killgore et al. 2007a). Nil-recapture estimates of Mississippi River population density may help assess the risk that recovery efforts (U.S. Fish and Wildlife Service 2014) will incur negative density-dependent effects on the wild population (Braaten et al. 2009).

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**Table 1.** Estimated total annual proportion of individuals dispersing to neighboring reaches, consistent with either uniform population density or the pattern of catch per unit effort (CPUE) observed during the survey. Converted from daily rates. Estimates for reaches C and D include both upstream and downstream movements.

Reach	Spatial Structure	
	Uniform	CPUE
B	0.41	0.26
C	0.53	0.59
D	0.34	0.31
MMR	0.15	0.15

**Table 2.** Lower-bound estimates of the abundance of age 3+ pallid sturgeon in the middle and lower Mississippi River for five model variations.

Model <sup>b</sup>	Abundance <sup>a</sup>		
	P = 0.99	P = 0.95	P = 0.75
Panmictic	4,100	6,300	14,000
Uniform	4,300	6,600	14,000
Uniform, dispersal	4,600	7,100	15,000
CPUE	4,800	7,400	16,000
CPUE, dispersal	5,000	7,700	17,000
Average of models	4,600	7,000	15,000

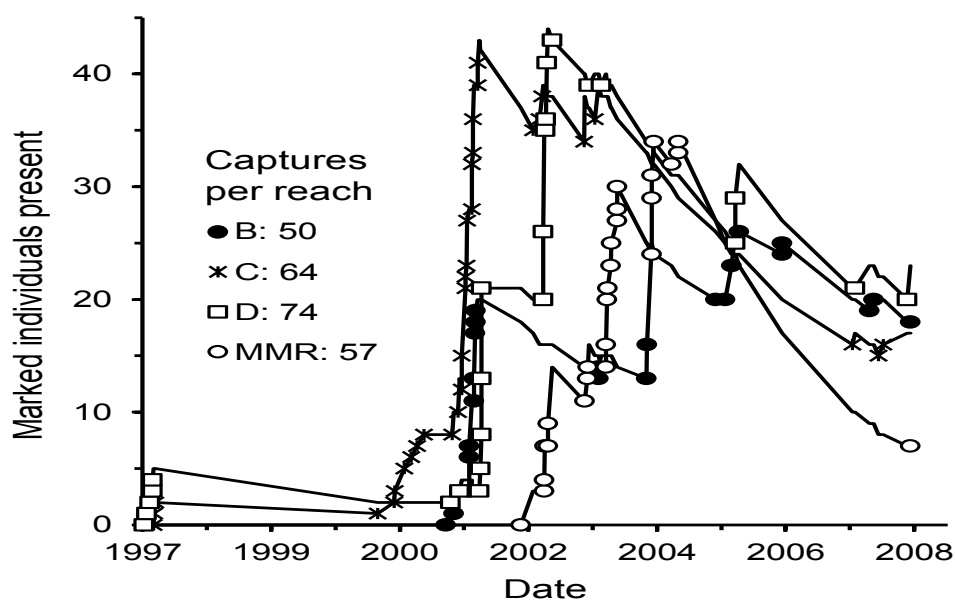
<sup>a</sup>Column headings give the approximate probability that the true abundance is not less than the estimates. Abundance rounded to two significant digits.

<sup>b</sup>Model variations described in Methods.

**Table 3.** Sensitivity of pallid sturgeon abundance estimates to annual emigration, based on the panmictic model results from Table 2.

Emigration	Abundance		
	$P = 0.99$	$P = 0.95$	$P = 0.75$
0%	4,800	7,400	16,000
10%	4,100	6,300	14,000
20%	3,400	5,200	11,300

Figure 1. Projected numbers of marked pallid sturgeon in four reaches of the middle and lower Mississippi River from 1997 through 2008. Symbols indicate dates on which individuals were caught and marked during the survey period (with the exception of the final symbol for the MMR, which was added to help identify the curve).



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Figure 2. The probability that the abundance of pallid sturgeon in the Mississippi River exceeds a range of lower bounds. Two sets of curves are shown. Each set corresponds to a Bayesian prior (uniform or Jeffreys). The three curves in each set demonstrate the effect of spatial structure model on the estimate. For uniform and CPUE models, curves indicate the estimate assuming no dispersal between reaches.

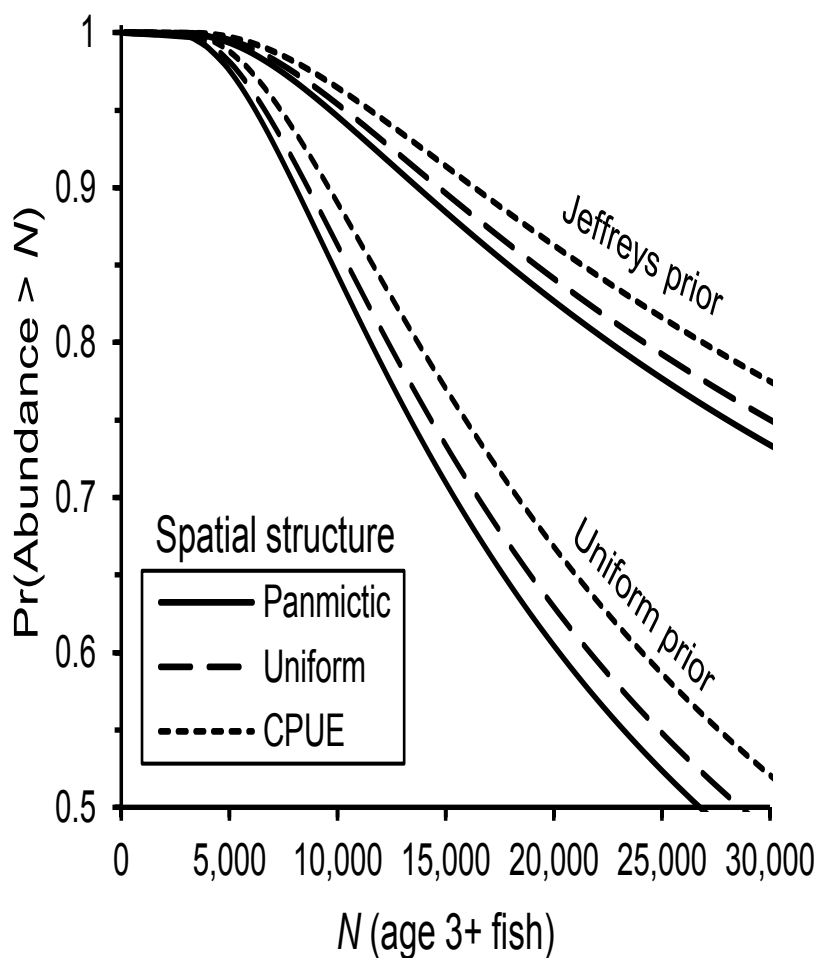


Figure 3. Spatial structure of pallid sturgeon abundance in the lower and middle Mississippi River. The two series in each panel reflect the results different spatial structure assumptions. (a) The 95% lower bound on population density. (b) The 95% lower bound on abundance.

