



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

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**Abstract:** *Abundance estimates are essential for assessing 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 devised a method for obtaining lower bounds on abundance in the absence of recaptures for both panmictic and spatially structured populations. The method assumes few enough recaptures were expected to be missed by random chance. The upper Bayesian credible limit on expected recaptures allows probabilistic statements about the minimum number of individuals present in the population. We applied this method to data from a 12-year survey of pallid sturgeon (*Scaphirhynchus albus*) in the lower and middle Mississippi River (U.S.A.). None of the 241 individuals marked was recaptured in the survey. After accounting for survival and movement, our model-averaged estimate of the total abundance of pallid sturgeon  $\geq 3$  years old in the study area had a 1%, 5%, or 25% chance of being  $< 4,600$ ,  $7,000$ , or  $15,000$ , respectively. When we assumed fish were distributed in proportion to survey catch per unit effort, the farthest 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/rkm for all model variations examined. The lower Mississippi River had an average density of pallid sturgeon  $\geq 3$  years old of at least 3.0–9.8 fish/rkm. The choice of Bayesian prior was the largest source of uncertainty we considered 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.*

**Keywords:** mark-recapture, nil recapture, population size, rare species, spatial structure

Estimación de la Abundancia sin Recapturas de Esturiones Pálidos Marcados en el Río Mississippi

**Resumen:** *Las estimaciones de abundancia son esenciales para evaluar la viabilidad de las poblaciones y los riesgos que presentan las acciones de manejo alternativo. Un esfuerzo para estimar la abundancia por medio de un experimento repetido de marcaje-recaptura puede fallar en la recaptura de individuos marcados. Diseñamos un método para obtener los límites inferiores de la abundancia en ausencia de recapturas para poblaciones panmixtas o estructuradas espacialmente. El método asume que se espera que suficientes recapturas mínimas no sean hechas por cuestiones de azar. El límite bayesiano superior confiable de recapturas esperadas permite afirmaciones probabilísticas sobre el número mínimo de individuos presentes en la población. Aplicamos este método a datos de un censo de 12 años del esturión pálido (*Scaphirhynchus albus*) en las partes media y baja del río Mississippi (E.U.A.). Ninguno de los 241 individuos marcados fue recapturado en este censo. Después de considerar la supervivencia y el movimiento, nuestro estimado promediado por el modelo de la abundancia total de esturiones pálidos  $\geq 3$  años de edad en el área de estudio tuvo un 1%, 5% ó 25% de probabilidad de ser  $< 4,600$ ,  $7,000$ , ó  $15,000$ , respectivamente. Cuando asumimos que los peces estaban distribuidos en proporción al esfuerzo de captura por unidad del censo, el alcance más lejano río abajo en el censo hospedó al menos a 4.5-15 peces por kilómetro de río (kmr), mientras que los*

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alcances restantes en las partes media y baja del río Mississippi hospedaron al menos a 2.6-8.5 peces/kmr para todo el modelo examinado. La parte baja del río Mississippi tuvo una densidad promedio de esturiones pálidos  $\geq 3$  años de edad de al menos 3.0-9.8/kmr. La elección del a priori bayesiano fue la mayor fuente de incertidumbre que consideramos pero no alteró el orden de magnitud de los límites inferiores. Los estimados de recaptura cero de la abundancia son altamente inciertos y requieren de una comunicación cuidadosa pero pueden proporcionar conocimiento a partir de experimentos que de otras formas podrían considerarse fracasos.

**Palabras Clave:** especies raras, estructura espacial, marcaje-recaptura, recaptura cero, tamaño poblacional

**摘要:** 度估计在评估种群生存力和评价管理风险方面至关重要。通过标记重捕实验进行丰度估计可能因没有重新捕获标记个体而失败。本研究提出了一种利用零重捕数据来估计种群丰度最小值的方法,并且这种方法对于随机交配种群和有遗传结构的种群均可适用。该方法假设由于随机事件造成的重捕量不足很少发生。这种方法可以根据期望重捕量的置信区间上限来推测种群数量并给出相应概率。我们利用该方法分析了一个持续 12 年的标志重捕调查数据集,估计了美国密西西比河中下游的浅色鲟鱼 (*Scaphirhynchus albus*) 的种群丰度。在调查中, 241 个标记个体都没再次被捕捉到。在考虑了死亡和迁移因素后, 模型给出了对该研究区域浅色鲟鱼种群个体 (>3 岁) 数量的估计: 有 1% 的概率低于 4600 条, 5% 的概率低于 7000 条以及 25% 的概率低于 15000 条。当假设真实鲟鱼密度与调查中的单位捕获量成比例时, 我们估计最远的一条下游河道中鲟鱼密度至少为 4.5-15 条/每条河每公里 (*rkm*), 而剩下的密西西比河中下游河道中鲟鱼密度至少为 2.6-8.5 条/*rKm*。密西西比河下游河道中浅色鲟鱼 (>3 岁) 的平均密度为至少 3.0-9.8 条/*rKm*。贝叶斯先验分布参数的选择是该方法分析结果不确定性的主要来源, 但它不会导致在估计种群丰度最小值时产生数量级上的误差。用零重捕数据估计丰度具有很大的不确定性, 并且在解读结果时需要非常小心, 但通过这种分析方法, 我们可以从以往被认为失败的标志重捕实验中获得有用信息。**翻译: 马天笑; 审校: 魏辅文**

**关键词:** 标志重捕, 零重捕, 珍稀动物, 种群大小, 空间结构

## 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 needed on rare species, an abundance estimate may be elusive. For instance, a mark-recapture experiment may fail to yield recaptures. We devised a method to infer lower bounds on abundance when no marked individuals are recaptured.

Intuitively, a mark-recapture experiment without recaptures could be remedied simply by continuing to sample. Although possibly impractical, this solution usefully casts recaptures as rare events that have not yet occurred. The need to estimate the probability of events that have not yet happened is far from novel and is, in fact, widespread. For example, engineers estimate the risk of failure of new oil-drilling equipment (Louis 1981) and doctors estimate the risk of adverse outcomes from a novel treatment (Smith & Winkler 1999; Winkler et al. 2002). 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-detections becomes information (Hanley & Lippman-Hand 1983; Jovanovic & Levy 1997; Andow et al. 2000).

Naively, the absence of recaptures suggests the focal population is very large because 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 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 2-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 been used in only 1 published study (Bell 1977).

We expanded the method of nil-recapture abundance estimation to repeated mark-recapture experiments (Schnabel 1938) in spatially structured populations. The use of Bayesian methods improves on the interpretation of results as well by allowing statements of the probability that actual abundance exceeds a lower bound. We explored the method and its sensitivities in a case study of the endangered pallid sturgeon (*Scaphirhynchus albus*) in the lower and middle Mississippi River in the United States. The resulting estimates, although highly imprecise, provide guidance on the lower bounds of abundance over a large portion of

the species' range despite the absence of recaptures in a 12-year study (Hoover et al. 2007; Killgore et al. 2007a, 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 and Marked Individuals

Let  $N$  be the estimate of total population size over all spatial units and  $N_j$  be the estimate for spatial unit  $j$ . We assumed 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 assumed 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 accounted 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. 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 expressed 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  $j$ :

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

The Poisson probability of no recaptures is then

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

Equation (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

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

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

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. With  $\chi^2$ ,

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

Estimates of  $N$  for particular levels of confidence can then be obtained with the  $\chi^2$  quantile function. We focused on the 99%, 95%, and 75% 1-tailed lower credible limits on abundance (examples in Supporting Information). Equation (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, although 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):

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

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

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

The inequality on the left 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 lower bound as the frequentist confidence limit (Eq. 5), whereas the Jeffreys reproduces that found with 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 (e.g., Winkler et al. 2002; 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 was listed as endangered in 1990 (U.S. Fish and Wildlife Service 1990) because of its presumed impacts to abundance and recruitment from 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, Louisiana (Dryer & Sandvol 1993). Pallid sturgeon may have once been common in the MMR. The LMR population is poorly documented and thought to be sparse (Duffy et al. 1996). However, the

abundance of pallid sturgeon relative to its sister species, *S. platyrhynchus*, 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 and the mouth of the Missouri River (Hoover et al. 2007; Killgore et al. 2007a, 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 is in Killgore et al. (2007a). Briefly, the survey data set 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. For the purposes of the survey the MMR was divided into two reaches, E and F. Here, we combined these reaches.

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. In all sampling bouts trotlines were used in a consistent manner. Each trotline was 61 m long, had 60 hooks baited with worms, and was deployed for approximately 16 hours 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. Pallid sturgeon that did not already have an internal passive integrated transponder tag were injected with one. Given the use of 2 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 was  $\geq 3$  years old.

We sought estimates of abundance in each of the river reaches, requiring constraints on spatial structure. Two sets of constraints were investigated. First, we 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. Second, we assumed spatial variation in population density was described by the reach-specific 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 and emigration.

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

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

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

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. platyrhynchus* there, which affected pallid sturgeon because its appearance is similar to *S. platyrhynchus*. 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. For our baseline model, we assumed 10% of fish emigrated annually and never returned. Sensitivity to the emigration rate was tested by evaluating abundance with 0% and 20% emigration.

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) and 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 (95% CI

0.024 to 0.143). We explored two levels of dispersal rates enclosing the 95% CI 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, whereas 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

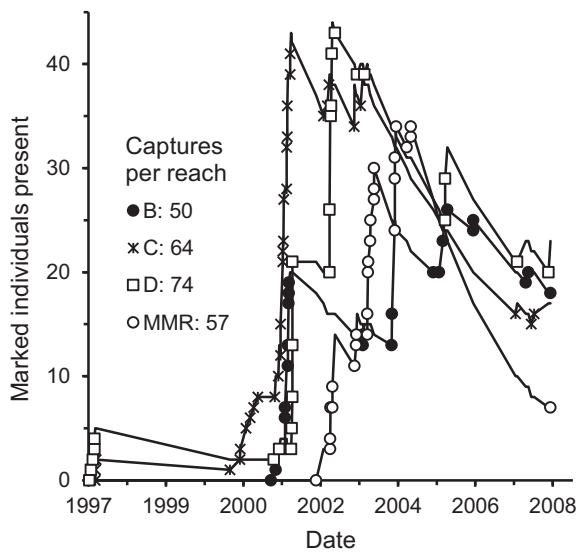
### Marked Individuals

In total, 50, 64, 70, and 57 pallid sturgeon were caught and marked in reaches B, C, D, and the MMR, respectively, from 1997 to 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 and reduced 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



**Figure 1.** Projected number of marked pallid sturgeon in 4 reaches of the middle and lower Mississippi River from 1997 to 2008 (B–D, river reaches). Symbols indicate dates on which individuals were caught and marked during the survey, with the exception of the final symbol for the middle Mississippi River (MMR), which was added to help visually differentiate data series.

**Table 1.** Estimated total annual proportional of individual pallid sturgeon dispersing to neighboring reaches consistent with either a uniform population density or the pattern of catch per unit effort (CPUE) observed during the survey.

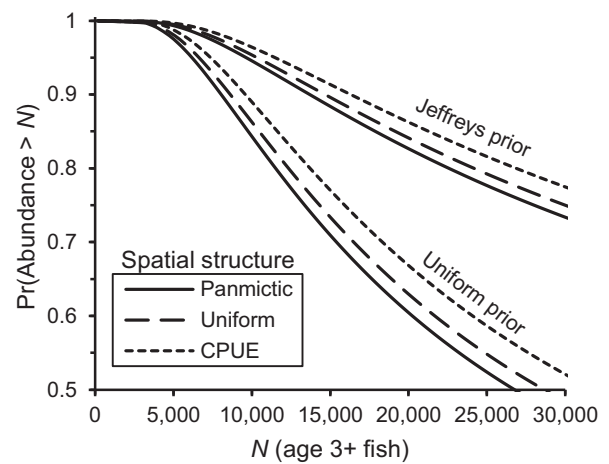
Reach	Spatial structure	
	uniform	CPUE
B	0.41	0.26
C <sup>b</sup>	0.53	0.59
D <sup>b</sup>	0.34	0.31
MMR <sup>c</sup>	0.15	0.15

<sup>a</sup>Converted from daily rates.

<sup>b</sup>Estimates include upstream and downstream movements.

<sup>c</sup>Middle Mississippi River.

Jeffreys prior produced a less rapid decline in support for larger population sizes than did the uniform prior (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 were more than 5,000 pallid sturgeon  $\geq 3$  years old in the Mississippi River was 0.984 and 0.996 with the uniform and Jeffreys prior, respectively. The remainder of the results were only for bounds found with the uniform prior because they were more conservative.



**Figure 2.** The probability that the abundance of pallid sturgeon in the Mississippi River exceeds a range of lower bounds. The 2 sets of curves correspond to a uniform and Jeffreys prior. The 3 curves in each set show the effect of spatial structure assumptions on the estimate. For uniform and catch-per-unit-effort (CPUE) spatial structures, curves indicate the estimate assuming no dispersal between river reaches.

**Table 2.** Lower-bound estimates of the abundance of pallid sturgeon  $\geq 3$  years in the middle and lower Mississippi River for 5 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 <sup>c</sup>	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 2 significant digits.

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

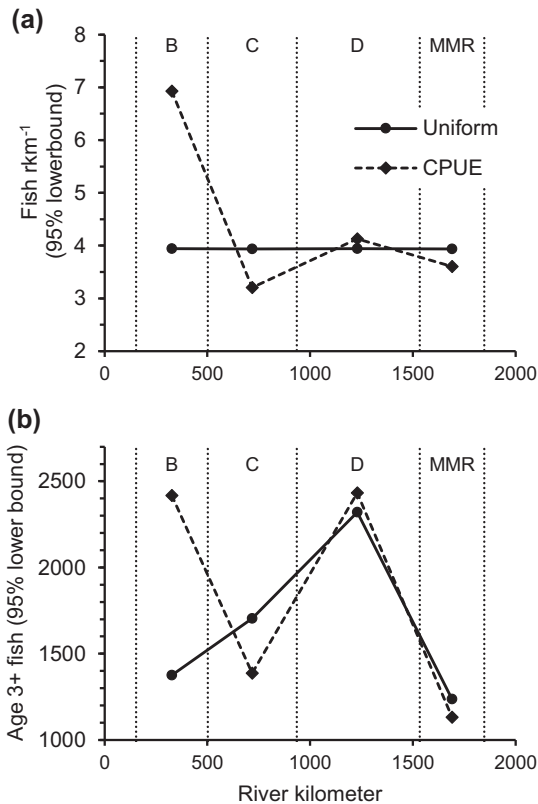
<sup>c</sup>Catch per unit effort.

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 fish  $\geq 3$  years old 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

**Table 3.** Pallid sturgeon abundance estimates relative 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 3.** Spatial structure of pallid sturgeon abundance in the lower and middle Mississippi River. The 2 series in each panel reflect different assumptions about spatial structure: (a) 95% lower bound on population density and (b) 95% lower bound on abundance (B–D, river reaches; MMR, middle Mississippi River;  $rkm$ , river kilometer).

recapture of one marked fish reported by commercial fishers in the Obion River, Tennessee (Killgore et al. 2007a). Baseline models conservatively assumed a 10% annual rate of emigration. A doubling of annual emigration to 20% decreased lower bounds by 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)

fish  $\geq 3$  years old 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)  $\geq 3$  years old (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) fish  $\geq 3$  years old  $rkm^{-1}$ , respectively (Fig. 3a). The CPUE model suggested a higher density in reach B of 6.5 (3.8–18.9)  $rkm^{-1}$ , which meant this estimate of total LMR density was higher than that of the MMR: 4.5 (3.0–9.8) fish  $\geq 3$  years old  $rkm^{-1}$  versus 3.6 (2.3–7.8) fish  $\geq 3$  years old  $rkm^{-1}$ , 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. Consider the finding that the average of our models suggested the population of pallid sturgeon  $\geq 3$  years old in the Mississippi River between New Orleans and the mouth of the Missouri River has a 99% probability of containing at least 4,600 individuals and a 75% probability of containing at least 15,000 individuals. Despite the careful wording, this statement may be misinterpreted as a confidence interval around the mean rather than as an uncertain lower 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 suggested a population of roughly 1,500 pallid sturgeon (Hintz et al. 2016), an estimate slightly above our 95% lower bound of 1,200–1,300 fish  $\geq 3$  years old and likely to include 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, although 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/ $rkm$  (Steffensen et al. 2012), in line with our lower bounds for the uniform Mississippi River population density of 2.6–8.5 fish  $\geq 3$  years old  $rkm^{-1}$ . 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.

Our nil-recapture estimates were 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. Although this sensitivity introduces an element of subjectivity to the estimation framework, Fig. 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 yielded a >98% chance that the population was larger than 5,000 individuals  $\geq 3$  years old. The nil-recapture focus on lower bounds may also be useful when the number of recaptures is very small because the central estimate can be biased in such cases (Chapman 1952).

Lower bounds on total abundance were also very sensitive to survival and emigration but 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 up- and downstream. 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 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). The rarity of younger age classes 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, and allows a fully Bayesian framework if desired.

Ultimately, lower bounds serve the specific purpose of answering the 1-tailed question of how small a population might be. An answer to this question 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 affected 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 on 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 considerably more dense than that of wild individuals (28.6–32.3 adult fish/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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## Supporting Information

The derivation of expected recaptures in multiple sub-populations (Eq. 1) and the expected rate of recaptures, as well as numerical examples with 1 and 2 populations (Appendix S1), are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.



## Literature Cited

- Andow DA, Olson DM, Hellmich RL, Alstad DN, Hutchinson W D. 2000. Frequency of resistance to *Bacillus thuringiensis* toxin Cry1Ab in and Iowa population of European corn borer (Lepidoptera: Crambidae). *Journal of Economic Entomology* **93**:26–30.
- Bailey RM, Cross FB. 1954. River sturgeons of the American genus *Scaphirhynchus*: characters, distribution, and synonymy. *Papers of the Michigan Academy of Science, Arts, and Letters* **39**:169–208.
- Bajer PG, Wildhaber ML. 2007. Population viability analysis of Lower Missouri River shovelnose sturgeon with initial application to the pallid sturgeon. *Journal of Applied Ichthyology* **23**:457–464.
- Baker J, Killgore KJ, Kasul R. 1991. Aquatic habitats and fish communities of the Lower Mississippi River. *Aquatic Sciences* **3**:313–356.
- Bell G. 1974. Population estimates from recaptures studies in which no recaptures have been made. *Nature* **248**:616.
- Bell G. 1977. The life of the smooth newt (*Triturus vulgaris*) after metamorphosis. *Ecological Monographs* **47**:279–299.
- Bernardo JM, Smith AFM. 1994. Bayesian theory. John Wiley and Sons, New York.
- Bettoli PW, Casto-Yerty M, Scholten GD, Heist EJ. 2009. Bycatch of the endangered pallid sturgeon (*Scaphirhynchus albus*) in a commercial fishery for shovelnose sturgeon (*Scaphirhynchus platyrhynchus*). *Journal of Applied Ichthyology* **25**:1–4.
- Braaten PJ, Fuller DB, Lott RD, Jordan GR. 2009. An estimate of the historic population size of adult pallid sturgeon in the upper Missouri River Basin, Montana and North Dakota. *Journal of Applied Ichthyology* **25**:2–7.
- Bramblett RG, White RG. 2001. Habitat use and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri rivers in Montana and North Dakota. *Transactions of the American Fisheries Society* **130**:1006–1025.
- Chao A, Lee SM, Teng SL. 1992. Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. *Biometrics* **48**:201–216.
- Chapman DG. 1952. Multiple sequential sample censuses. *Biometrics* **8**:286–306.
- Chapman DG. 1954. Estimation of biological populations. *The Annals of Mathematical Statistics* **25**:1–15.
- Dryer MP, Sandvol AJ. 1993. Recovery plan for the pallid sturgeon (*Scaphirhynchus albus*). U.S. Fish and Wildlife Service, Denver.
- Duffy WG, Berry CR, Keenlyne KD. 1996. The pallid sturgeon: biology and an annotated bibliography through 1994. Technical bulletin 5. South Dakota Cooperative Fish and Wildlife Research Unit, South Dakota State University, Brookings.
- Edwards AWF. 1974. Population estimates from recapture studies. *Nature* **252**:509–510.
- Ferson S, Burgman MA, editors. 2000. Quantitative methods for conservation biology. Springer, New York.
- Forbes SA, Richardson RE. 1905. On a new shovelnose sturgeon from the Mississippi River. *Bulletin of the Illinois State Laboratory of Natural History* **7**:37–44.
- Garwood F. 1936. Fiducial limits for the Poisson distribution. *Biometrika* **28**:437–442.
- Gelman A. 2006. Prior distributions for variance parameters in hierarchical models. *Bayesian Analysis* **1**:515–533.
- Hanley JA, Lippman-Hand A. 1983. If nothing goes wrong, is everything all right? *JAMA* **249**:1743–1745.
- Hilborn R. 1990. Determination of fish movement patterns from tag recoveries using maximum-likelihood estimators. *Canadian Journal of Fisheries and Aquatic Sciences* **47**:635–643.
- Hintz WD, Glover DC, Garvey JE, Killgore KJ, Herzog DP, Spier TW, Colombo RE, Hrabik RA. 2016. Status and habitat use of *Scaphirhynchus* sturgeons in an important fluvial corridor: implications for river habitat enhancement. *Transactions of the American Fisheries Society* **145**:386–399.
- Hoover JJ, George SG, Killgore KJ. 2007. Diet of shovelnose sturgeon and pallid sturgeon in the free-flowing Mississippi River. *Journal of Applied Ichthyology* **23**:494–499.
- Hudson DJ. 1971. Interval estimation from the likelihood function. *Journal of the Royal Statistical Society. Series B (Methodological)* **33**:256–262.
- Jaynes ET. 1976. Confidence intervals vs Bayesian intervals. Pages 175–257 in Harper WL, Hooker CA, editors. *Foundations of probability theory, statistical inference, and statistical theories of science*. D. Reidel Publishing, Dordrecht, Netherlands.
- Jovanovic B, Levy P. 1997. A look at the rule of three. *The American Statistician* **51**:137–139.
- Kerman J. 2011. Neutral noninformative and informative conjugate beta and gamma prior distributions. *Electronic Journal of Statistics* **5**:1450–1470.
- Killgore KJ, Hoover JJ, George SG, Lewis BR, Murphy CE, Lancaster WE. 2007a. Distribution, relative abundance and movements of pallid sturgeon in the free-flowing Mississippi River. *Journal of Applied Ichthyology* **23**:476–483.
- Killgore KJ, Hoover JJ, Kirk JP, George SG, Lewis BR, Murphy CE. 2007b. Age and growth of pallid sturgeon in the free-flowing Mississippi River. *Journal of Applied Ichthyology* **23**:452–456.
- Koch B, Brooks RC, Oliver A, Herzog D, Garvey JE, Hrabik R, Colombo R, Phelps Q, Spier T. 2012. Habitat selection and movement of naturally occurring pallid sturgeon in the Mississippi River. *Transactions of the American Fisheries Society* **141**:112–120.
- Louis TA. 1981. Confidence intervals for a binomial parameter after observing no successes. *The American Statistician* **35**:154.
- Mayden RL, Kuhajda BR. 1997. Threatened fishes of the world: *Scaphirhynchus albus* (Forbes & Richardson, 1905) (Acipenseridae). *Environmental Biology of Fishes* **48**:420–421.
- Morris WF, Doak DF. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts.
- Neyman J. 1937. Outline of theory of statistical estimation based on the classical theory of probability. *Philosophical Transactions of the Royal Society of London A* **236**:333–380.
- Otis DL, Burnham KP, White GC, Anderson DR. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62**:3–135.
- Schnabel ZE. 1938. The estimation of total fish population of a lake. *The American Mathematical Monthly* **45**:348–352.
- Smith JE, Winkler RL. 1999. Casey's problem: interpreting and evaluating a new test. *Interfaces* **29**:63–76.
- Steffensen KD, Powell LA, Koch JD. 2010. Assessment of hatchery-reared pallid sturgeon survival in the lower Missouri River. *North American Journal of Fisheries Management* **30**:671–678.
- Steffensen KD, Powell LA, Pegg MA. 2012. Population size of hatchery-reared and wild pallid sturgeon in the lower Missouri River. *North American Journal of Fisheries Management* **32**:159–166.
- U.S. Fish and Wildlife Service. 1990. Determination of endangered status for the pallid sturgeon. *Federal Register* **55**:36641–36647.
- U.S. Fish and Wildlife Service. 2014. Revised recovery plan for the pallid sturgeon (*Scaphirhynchus albus*). Northern Rockies Fish and Wildlife Conservation Office, Denver.
- Webster AJ, Kemp R. 2013. Estimating commissions from searches. *The American Statistician* **67**:82–89.
- Wilks SS. 1938. The large-sample distribution of the likelihood ratio for testing composite hypotheses. *The Annals of Mathematical Statistics* **9**:60–62.
- Williams BK, Nichols JD, Conroy MJ. 2002. Analysis and management of animal populations. Academic Press, San Diego, California.
- Winkler RL, Smith JE, Fryback DG. 2002. The role of informative priors in zero-numerator problems: being conservative versus being candid. *The American Statistician* **56**:1–4.