Brief Communication

Retention of Ancestral Genetic Variation Across Life-Stages of an Endangered, Long-Lived Iteroparous Fish


From the Biology Department and Museum of Southwestern Biology, University of New Mexico, MSC03 2020, 1 University of New Mexico Way, Albuquerque, NM 87131-0001 (Carson, Pilger, and Turner); School of Life Sciences, PO Box 874501, Arizona State University, Tempe, AZ 85287-4501 (Adams, Dowling, Marsh, and Saltzgiver); and Marsh & Associates, LLC, Tempe, AZ 85282-6845 (Kesner and Marsh). Dowling and Saltzgiver is now at the Department of Biological Sciences, Wayne State University, Detroit, MI 48202-3917.

Address correspondence to Evan W. Carson at the address above, or e-mail: evan.carson@gmail.com.

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Abstract

As with many endangered, long-lived iteroparous fishes, survival of razorback sucker depends on a management strategy that circumvents recruitment failure that results from predation by non-native fishes. In Lake Mohave, AZ-NV, management of razorback sucker centers on capture of larvae spawned in the lake, rearing them in off-channel habitats, and subsequent release (“repatriation”) to the lake when adults are sufficiently large to resist predation. The effects of this strategy on genetic diversity, however, remained uncertain. After correction for differences in sample size among groups, metrics of mitochondrial DNA (mtDNA; number of haplotypes, \( N_H \), and haplotype diversity, \( H_D \)) and microsatellite (number of alleles, \( N_A \), and expected heterozygosity, \( H_E \)) diversity did not differ significantly between annual samples of repatriated adults and larval year-classes or among pooled samples of repatriated adults, larvae, and wild fish. These findings indicate that the current management program thus far maintained historical genetic variation of razorback sucker in the lake. Because effective population size, \( N_e \), is closely tied to the small census population size \( (N_c \approx 1500–3000) \) of razorback sucker in Lake Mohave, this population will remain at risk from genetic, as well as demographic risk of extinction unless \( N_c \) is increased substantially.

Management of endangered species often focuses on reducing extinction risk by increasing census size, \( N_c \), while also retaining or increasing genetic diversity and effective population size, \( N_e \) (Ryman and Laikre 1991). Although the relationships between \( N_c \) and extinction risk are most closely associated with vulnerability to demographic and environmental stochasticity (Allendorf and Luikart 2007), genetic risks of extinction are determined primarily by relationships of genetic diversity and \( N_e \) to the average fitness of a population (Reed and Frankham 2003) and to the potential of a population to adapt to changed environments (Reed and Frankham 2003; Allendorf and Luikart 2007). The difference is important because management actions that reduce one risk can inadvertently
increase the other. Hatchery-based supplementation of wild populations, for example, can increase $N_e$ yet reduce $N_m$ if large numbers of closely related individuals are released to the wild (Ryman and Laikre 1991). Demographic and genetic responses to management actions, therefore, often need to be evaluated together (Osborne et al. 2012; Duong et al. 2013).

These challenges are exemplified in management of endangered razorback sucker, *Xyrauchen texanus* (USFWS 1991). This large, long-lived catostomid was abundant and widespread in the Colorado River basin, southwestern United States, (McAda and Wydoski 1980; Minckley 1983) until habitat alterations in the mid-20th century led to steep declines in abundance of the species (Minckley et al. 1991). Although predation by non-native fishes caused complete recruitment failure in the wild (Marsh et al. 2003), the longevity of razorback sucker (>50 years) ensured persistence of a large census population size ($N > 50,000$) until the mid-1990s, when a sharp population decline occurred as old fish died off (Marsh et al. 2015).

A conservation program for razorback sucker in Lake Mohave, AZ-NV, began in the early 1990s (Minckley et al. 1991; Marsh et al. 2015) after a strategy was developed to circumvent recruitment failure in the wild (Marsh et al. 2005). Briefly, each spring larvae collected in the lake are reared in hatcheries and off-channel grow-out facilities. When fish reach sub-adult size or larger, they are tagged with a passive integrated transponder (PIT) and returned (hereafter termed “repatriated adults”) to the lake (Marsh et al. 2015). The parental pool for razorback sucker in Lake Mohave, therefore, is represented by repatriated adults and (until recently) remaining wild fish. From 1997 to 2010 more than 140,000 razorback sucker were repatriated to Lake Mohave, and over this period $N_m$ remained relatively stable, ranging from ~1000 to ~3000 individuals (Dowling et al. 2014). Although the strategy arrested decline of the population, survival of released fish remains low (Karam et al. 2010; Kesner et al. 2012) and natural recruitment still does not occur (Minckley 1983; Minckley et al. 1991; Marsh et al. 2015).

Annual genetic monitoring of larval razorback sucker collected from 1997 to 2010 showed a slight increase in genetic diversity for mitochondrial DNA (mtDNA) and stability of variation at microsatellite loci (Dowling et al. 2014). The increase in effective number of breeders, $N_e$, over this period suggested that management actions reduced variance in reproductive success in the population. Little was known, however, about the relationship of genetic variation among repatriated adults, larval year-classes, and the remaining wild fish that recruited naturally (Dowling et al. 2005). This is complicated in part because the contribution of wild fish to larval year classes (which are raised in protected off-channel habitats) declined while the reproductive contribution of repatriated adults increased from 1997 to 2010 (i.e., the parental pool has changed over time; see Figure 4 of Marsh et al. 2015 for visualization of this dramatic change). If genetic diversity does not differ significantly among larvae, repatriated adults, and wild fish, then management actions would be deemed effective in preserving genetic variation of the species. If, however, genetic diversity differs significantly among these groups, then current management actions may be inadequate for maintaining genetic variation over time if genetic drift is increased or if non-neutral processes, such as nonrandom survival, hatchery-induced selection, or relaxation of selection pressures in the wild, are important.

This study assessed the effects of management actions on genetic diversity of razorback sucker in Lake Mohave. We used samples collected annually from 1997 to 2010 to survey variation in mitochondrial DNA sequences and nuclear-encoded microsatellite DNA loci in mixed-age repatriated adults, larval year-classes, and a pooled collection of mixed-age wild fish. We asked 1) Is genetic diversity statistically equivalent between annual samples of repatriated adults and larval year-classes? and 2) Is genetic variation of wild, naturally recruited adults maintained in repatriated adults and larvae? After correction for differences in sample size among groups, significant differences would indicate that effects of non-neutral processes, including nonrandom differences in survival and reproductive success, may be important, whereas nonsignificance would suggest that the current management program thus far has maintained genetic variation of the wild fish. We discuss findings in the context of management of razorback sucker in Lake Mohave and other endangered, long-lived iteroparous freshwater fishes.

**Materials and Methods**

**Sampling for Molecular Analyses**

From 1997 to 2010, we collected a total of 6943 razorback sucker, including 5893 larvae, 747 repatriated adults, and 303 wild adults, from Lake Mohave, AZ-NV. Sampling was conducted during the spawning season (January to April). Repatriated adults and wild fish were captured in trammel nets deployed near sites where Dowling et al. (2014) collected larvae. Identification of recaptured specimens was based on the unique 10-digit passive integrated transponder (PIT) tag that was implanted when each fish was first captured or released; for detailed description of the methodology, see Marsh et al. (2005). Tissues were collected as fin clips (<1 g) from adult fish or as whole larva and preserved in 95% ethanol. The modified phenol-chloroform protocol of Tibbets and Dowling (1996) was used to extract genomic DNA.

**Definition of Year Classes and Cohorts**

Each larval year-class was composed of individuals from a single cohort collected in a single year in Lake Mohave, with a total of 14 larval year-classes collected from 1997 to 2010. Repatriated adults could not be assigned by year-class because these fish were kept in captivity for different lengths of time prior to release. Because “cohorts” of repatriated adults were assigned based on the year fish were stocked into the lake, most were composed of multiple age groups (Supplementary Table S1).

**Mitochondrial DNA**

mtDNA sequence variation was evaluated for a 311-bp fragment of the 3’ end of cytochrome b (*cytb*). Haplotype data for larvae (n = 230–571 per cohort; n = 5893 total) were obtained from Dowling et al. (2014). Sequences for repatriated adult cohorts (n = 16–92 among samples; n = 747 total) and wild fish (n = 301 total) are reported for the first time; there were no new haplotypes beyond those reported in Dowling et al. (2014). Number of haplotypes ($N_h$) and haplotype diversity ($H_b$) were assessed in Arlequin 3.5.1.2 (Excoffier and Lischer 2010), and Analytic Rarefaction 1.3 (Holland 2003) was used to correct for differences in sample size ($H_b$).

**Microsatellites**

We used 13 microsatellite loci (Turner et al. 2009; Dowling et al. 2012a) to survey genetic variation in larvae (n = 1680), repatriated adults (n = 736), and wild fish (n = 303). Microsatellite genotypes of larvae, a random subsample of 120 individuals per year-class, were reported in Dowling et al. (2014). Sample sizes for cohorts of repatriated adults ranged from 16 to 86 individuals, depending on year sampled (1997–2010). Wild fish represented fish that recruited...
naturally to the population and included only a pooled sample of fish that were collected from 1997 to 2010.

Analysis of microsatellites followed methods used by Dowling et al. (2012a, 2012b). Departures from Hardy–Weinberg proportions (HWP) and multilocus equilibrium were examined using exact probability tests as implemented in GenePop (Raymond and Rousset 1995); tests were conducted using the Markov Chain method (Guo and Thompson 1992), with parameters of 10 000 dememorizations, 500 batches, and 5000 iterations per batch. For each larval year-class, repatriated adult cohort, and the pooled sample of wild fish, number of alleles (\(N_a\)), allelic richness (\(A_r\)), and gene diversity (\(H_e\)) were calculated using F-Stat version 2.9.3.2 (Goudet 2001). Homogeneity in allelic richness and gene diversity between annual samples of repatriated adults and larval year-classes was assessed with Wilcoxon signed-rank tests as implemented in SPSS 23 (IBM, Armonk, NY). For comparisons among repatriated adults, larvae, and wild fish, samples of each group were pooled and homogeneity in allelic richness and gene diversity were evaluated (by locus) with Friedman rank tests, also as implemented in SPSS.

For each larval cohort sampled from 1997 to 2010, effective number of breeders, \(N_e\), was estimated with the linkage disequilibrium method LDNE of Waples and Do (2008) as implemented in NeEstimator V2.01 (Do et al. 2014); LDNE corrects for downward bias on \(N_e\) when sample size is less than true \(N_e\) (Waples 2006). Harmonic \(N_e\) across the same period was calculated based on the relationship \(N_e = N_r \cdot N_s\) in razorback sucker (Waples et al. 2013). Generational \(N_e\) of pooled samples of repatriated adults, larvae, and wild fish also was calculated. Variance effective population size, \(N_{ve}\), of adjacent larval year-classes was calculated in TempoFS (Jorde and Ryman 2007) under sampling Plan II (i.e., sampling before reproduction and without replacement; Waples 1989) as implemented in NeEstimator; TempoFS is an unbiased estimator of \(N_{ve}\). The method of Jorde and Ryman (1995, 1996) was used to correct for overlapping generations, where \(C = 40.37\) and \(G = 9.03\) for razorback sucker (Turner et al. 2007; Dowling et al. 2014). Generational \(N_{ve}\) calculated (without correction) from the 1997 and 2010 pair of larval cohorts. Estimates were based on the 2% threshold for exclusion of rare alleles to achieve precise, largely unbiased estimates of \(N_e\) from highly polymorphic markers (Waples and Do 2010) and to correct for upward bias that skewed allele frequencies and small sample sizes introduce to estimates of \(N_{ve}\) (Waples 1989; Jorde and Ryman 2007). The jackknife method was used to calculate 95% confidence intervals (CIs) for all estimates.

Data Archiving

In fulfillment of data archiving requirements for Journal of Heredity (Baker 2013), all underlying data for this study are included as Supplementary Material or deposited at Dryad (http://dx.doi.org/10.5061/dryad.cf730).

Results

Mitochondrial DNA

Summary statistics, including number of haplotypes, haplotype diversity, and haplotype richness for larvae, repatriated adults, and wild fish, are shown in Table 1. From 1997 to 2010, a total of 34 mtDNA haplotypes were observed among all life stages, including \(N_{h} = 34\) for larvae (14 [2001, 2002] to 22 [2006]), \(N_{h} = 26\) for repatriated adults (4 [2002] to 12 [1998]), and \(N_{h} = 18\) for wild adults (pooled sample). Among years, average haplotype diversity of larvae ranged from \(H_{D} = 0.512\) [2002] to 0.696 [2009] and of repatriated adults ranged from \(H_{D} = 0.363\) [2002] to 0.792 [2008]. Across years (i.e., pooled collections), haplotype diversity was \(H_{D} = 0.602\) for larvae, \(H_{D} = 0.576\) for repatriated adults, and \(H_{D} = 0.628\) for wild fish. Based on 95% CIs from rarefaction, differences in haplotype diversity, and richness, and haplotype richness for larvae, repatriated adults, and wild fish sampled annually from 1997 to 2010, where \(n\) is sample size mtDNA/microsatellites

Table 1. Summary statistics for mitochondrial DNA (mtDNA) and microsatellite DNA variation in repatriated adults, larvae, and wild fish sampled annually from 1997 to 2010, where \(n\) is sample size mtDNA/microsatellites

<table>
<thead>
<tr>
<th>Year</th>
<th>(n)</th>
<th>(N_{H})</th>
<th>(H_{D})</th>
<th>(N_{A})</th>
<th>(A_{K})</th>
<th>(H_{E})</th>
<th>(n)</th>
<th>(N_{H})</th>
<th>(H_{D})</th>
<th>(N_{A})</th>
<th>(A_{K})</th>
<th>(H_{E})</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>28/28</td>
<td>6</td>
<td>0.439</td>
<td>11.8</td>
<td>10.1</td>
<td>0.751</td>
<td>338/120</td>
<td>18</td>
<td>0.633</td>
<td>15.8</td>
<td>10.1</td>
<td>0.745</td>
</tr>
<tr>
<td>1998</td>
<td>82/82</td>
<td>12</td>
<td>0.468</td>
<td>14.5</td>
<td>10.2</td>
<td>0.745</td>
<td>484/120</td>
<td>19</td>
<td>0.547</td>
<td>15.2</td>
<td>10.1</td>
<td>0.731</td>
</tr>
<tr>
<td>1999</td>
<td>69/69</td>
<td>11</td>
<td>0.564</td>
<td>14.1</td>
<td>10.0</td>
<td>0.746</td>
<td>291/120</td>
<td>15</td>
<td>0.517</td>
<td>15.4</td>
<td>9.9</td>
<td>0.738</td>
</tr>
<tr>
<td>2000</td>
<td>66/65</td>
<td>10</td>
<td>0.443</td>
<td>14.2</td>
<td>10.4</td>
<td>0.757</td>
<td>366/120</td>
<td>17</td>
<td>0.589</td>
<td>15.8</td>
<td>9.9</td>
<td>0.719</td>
</tr>
<tr>
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<td>39/39</td>
<td>10</td>
<td>0.723</td>
<td>13.2</td>
<td>10.4</td>
<td>0.739</td>
<td>230/120</td>
<td>14</td>
<td>0.620</td>
<td>15.7</td>
<td>10.3</td>
<td>0.732</td>
</tr>
<tr>
<td>2002</td>
<td>20/20</td>
<td>4</td>
<td>0.363</td>
<td>9.9</td>
<td>9.5</td>
<td>0.739</td>
<td>344/120</td>
<td>14</td>
<td>0.512</td>
<td>15.5</td>
<td>10.1</td>
<td>0.738</td>
</tr>
<tr>
<td>2003</td>
<td>22/23</td>
<td>6</td>
<td>0.636</td>
<td>11.5</td>
<td>10.6</td>
<td>0.735</td>
<td>370/120</td>
<td>18</td>
<td>0.638</td>
<td>15.5</td>
<td>10.1</td>
<td>0.739</td>
</tr>
<tr>
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<td>10</td>
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<td>14.1</td>
<td>10.0</td>
<td>0.753</td>
<td>559/120</td>
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<td>10.0</td>
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<td>10.2</td>
<td>0.731</td>
<td>437/120</td>
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<td>0.606</td>
<td>15.5</td>
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</tr>
<tr>
<td>2006</td>
<td>37/37</td>
<td>7</td>
<td>0.602</td>
<td>12.2</td>
<td>9.6</td>
<td>0.728</td>
<td>571/120</td>
<td>22</td>
<td>0.614</td>
<td>15.4</td>
<td>9.9</td>
<td>0.727</td>
</tr>
<tr>
<td>2007</td>
<td>43/42</td>
<td>11</td>
<td>0.630</td>
<td>13.2</td>
<td>10.4</td>
<td>0.754</td>
<td>308/120</td>
<td>20</td>
<td>0.645</td>
<td>15.5</td>
<td>10.0</td>
<td>0.737</td>
</tr>
<tr>
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<td>16/16</td>
<td>6</td>
<td>0.792</td>
<td>8.7</td>
<td>9.3</td>
<td>0.738</td>
<td>602/120</td>
<td>21</td>
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<td>16.1</td>
<td>10.4</td>
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<td>0.641</td>
<td>14.5</td>
<td>9.9</td>
<td>0.738</td>
<td>515/120</td>
<td>19</td>
<td>0.696</td>
<td>15.6</td>
<td>10.0</td>
<td>0.745</td>
</tr>
<tr>
<td>2010</td>
<td>92/86</td>
<td>12</td>
<td>0.574</td>
<td>14.8</td>
<td>9.9</td>
<td>0.732</td>
<td>478/120</td>
<td>19</td>
<td>0.587</td>
<td>14.8</td>
<td>9.9</td>
<td>0.739</td>
</tr>
<tr>
<td>Total/Ave</td>
<td>747/736</td>
<td>9.1</td>
<td>0.575</td>
<td>12.9</td>
<td>0.742</td>
<td>5893/1680</td>
<td>18.2</td>
<td>0.598</td>
<td>15.5</td>
<td>0.735</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

For mtDNA only, \(N_{h}\) is number of haplotypes and \(H_{D}\) haplotype diversity. For microsatellites only, \(N_{h}\) is number of alleles, \(A_{K}\) is allelic richness, and \(H_{E}\) is expected heterozygosity (gene diversity).
richness were nonsignificant for comparisons between annual samples of repatriated adults and larvae (1997–2010) and annual samples of repatriated adults (1997–2010) and between annual samples of repatriated adults and the pooled sample of wild fish.

**Microsatellites**

Significant deviation from HWP was observed in 56 of 182 tests (30.8%) for larvae, 42 of 182 tests for repatriated adults, and 24 tests (13.2%) for larvae, 16 tests (8.8%) for repatriated adults, simultaneously (Narum 2006), significant deviations remained in 30.8% for larvae, 42 of 182 tests for repatriated adults (23.1%) and significant deviation from HWP was observed in 56 of 182 tests revealed the same effect for repatriated adult cohorts, where deviations from HWP in larval stemsmed from an analysis strategy that combined individuals collected from independent spawning locations and times (i.e., a Wahlund effect) and not from problems inherent to individual loci. A positive association between number of alleles at a locus and deviation from HWP also was found. This study revealed the same effect for repatriated adult cohorts, where deviations from HWP stemmed from sampling fish that were derived from mixed samples of larvae and was reared in the hatchery initially and in raceways or off-channel habitats in later years of the program. In addition, because repatriated adult cohorts and the pooled sample of wild fish each were composed of multiple year classes, age structure potentially contributed to deviations from HWP, as age structure is known to create Wahlund-like effects in single populations that exhibit random mating (Waples 2015). For these reasons, we retained the original set of 13 loci for subsequent analyses.

Summary statistics, including average number of alleles per locus, allelic richness, and gene diversity for larvae, repatriated adults, and wild fish, are shown in Table 1. Across all collections (1997–2010 pooled), the average number of alleles per locus was $N_a = 20.1$ (range of 14.8 [2010] to 16.1 [2008] from annual samples) for larvae; $N_a = 18.8$ (range of 8.7 [2008] to 14.8 [2005, 2010] from annual samples) for repatriated adults; and $N_a = 16.9$ for wild fish (pooled sample). Across all collections (1997–2010), comparisons between allelic richness of larvae ($A_a$ = 9.9 [1999] to 10.4 [2008]) and repatriated adults ($A_a$ = 9.3 [2008] to 10.6 [2003]) and between gene diversity of larvae ($H_e$ = 0.719 [2000]) to 0.745 [2009]) and repatriated adults ($H_e$ = 0.728 [2006] to 0.757 [2000]) did not differ significantly (Wilcoxon signed-rank test, $P$-value = 0.730 for $A_a$ and $P$-value = 0.074 for $H_e$). Similarly, for comparisons (among loci) of allelic richness and gene diversity ($A_a$ = 19.4; $H_e$ = 0.738), repatriated adults ($A_a = 19.5; H_e = 0.745$), and wild fish ($A_a = 19.1; H_e = 0.745$) also were nonsignificant (Friedman Test, $P$-value = 0.138 for $A_a$ and $P$-value = 0.923 for $H_e$).

Estimates of $N_c$ (= $N_e$) for larval cohorts ranged from $N_c = 313$ (2001) to $N_c = 49$, 984 (2005), with a harmonic mean of $N_c = 826$ (Table 2 and Supplementary Figure S1). Estimates of generational $N_c$ (pooled samples) were $N_c = 3362$ (95% CI 2545–4802) from larvae; $N_c = 1928$ (95% CI 1423–2896) from repatriated adults; and $N_c = 1520$ (95% CI 932–3748) from wild fish. Variance effective size of larval cohorts ranged from $N_v = 98$ (2008–2009) to $N_v = 1238$ (2004–2005), with generational $N_v = 460$ (95% CI 172–∞; Table 2 and Supplementary Figure S2).

**Discussion**

From 1997 to 2010, $N_e$, $N_c/N_e$, and mtDNA diversity increased significantly in razorback sucker in Lake Mohave (Dowling et al. 2014) despite precipitous decline in $N_e$ over the same period (Marsh et al. 2015). The effects of management actions on genetic variation remained uncertain, however, because little was known about the relationship of genetic diversity among repatriated adult cohorts, larval year classes, and wild adults. Our study demonstrated that genetic diversity of mtDNA and microsatellites did not differ significantly between cohorts of repatriated adults and respective larval year classes sampled from 1997 to 2010 or among pooled samples of repatriates, larvae, and wild fish collected over the same period. These findings suggest that over the period of our study the repatriation program maintained genetic variation of the (now extirpated) wild population and, importantly, that effects of non-neutral processes (e.g., non-random selection, hatchery-induced selection, or relaxation of selection pressures in the wild) were negligible.

Root causes of risk of extinction from demographic and genetic effects differ but the relationship between these determinants is important. For razorback sucker in Lake Mohave, from 1997 to 2010 there was near-parity of $N_c$ (~1500–3000) and generational $N_c$ of larvae ($N_c = 3362$), repatriated adults ($N_c = 1928$), and wild fish ($N_c = 1520$) and harmonic $N_c = 826$ of larval cohorts. This suggests that current management actions influence these metrics similarly. If so, $N_c$ should respond positively to increases in $N_e$, as should inbreeding effective size since $N_c/N_e = 1.0$ for razorback sucker (see supplementary table S2 in Waples et al. 2013). This, however, also suggests that increases in $N_c$ and, thus, $N_e$ are unlikely to occur under the current management strategy unless $N_c$ is increased substantially. While estimates of $N_c$ are sufficiently large to allay concerns over inbreeding depression (Rieman and Allendorf 2001), variance effective population size, $N_{ve}$, typically was <500 for larval year-classes sampled from 1997 to 2010 (as also reported by Dowling et al. 2014), with generational $N_{ve} = 460$ over this period. This rate of genetic drift raises concern that the population is at risk of loss of adaptive variation over time (Rieman and Allendorf 2001). If $N_{ve}$ and $N_{ve}$ respond similarly to management actions, then this risk also is likely to persist until $N_c$ is increased.

Concerns over demographic and genetic risks of low $N_c$ are not new (Marsh et al. 2015). A plausible strategy to bolster $N_c$ was outlined by Minckley et al. (2003). Under their plan, isolated backwater habitats would hold razorback sucker (and other native fishes) in natural habitats that are free of non-native fishes (i.e., predators). This strategy is part of the species’ recovery plan (USFWS 2005), and steps toward its implementation are being taken by the MSCP (LCR MSCP 2004).

Few studies have documented the relationships between genetic and demographic characteristics of long-lived, iteroparous freshwater fishes (Lippé et al. 2006; Duong et al. 2013; Dowling et al. 2014), yet this information can be crucial to their conservation. This is particularly important for fishes such as paddlefish (Sloss et al. 2009), razorback sucker (Dowling et al. 2014), and sturgeon (Jay et al. 2014), among others, where conservation depends upon supportive breeding because recruitment in the wild is low or absent. Our study advances management of razorback sucker in Lake Mohave by clarifying the relationship between genetic diversity of repatriated adult cohorts and larval year-classes and the relationship of genetic diversity of wild fish to larvae and repatriated adults. This improves understanding of genetic risk of extinction, resolves questions over success of management actions in maintaining historical genetic variation of the species, and, by demonstrating a close relationship of
Table 2. Estimates of effective number of breeders, \( N_e \), and variance effective population size, \( N_{ve} \), calculated from larvae collected annually from 1997 to 2010.

<table>
<thead>
<tr>
<th>Cohort</th>
<th>( N_e ) (( N_{ve} ))</th>
<th>lci</th>
<th>uci</th>
<th>Paired-cohorts</th>
<th>( N_e ) (( N_{ve} ))</th>
<th>lci</th>
<th>uci</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>643</td>
<td>400</td>
<td>1522</td>
<td>1999–2000</td>
<td>139</td>
<td>94</td>
<td>273</td>
</tr>
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<td>2006</td>
<td>669</td>
<td>371</td>
<td>2670</td>
<td>2006–2007</td>
<td>376</td>
<td>237</td>
<td>952</td>
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<tr>
<td>2007</td>
<td>1,873</td>
<td>653</td>
<td>∞</td>
<td>2007–2008</td>
<td>353</td>
<td>156</td>
<td>∞</td>
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<td>2008</td>
<td>671</td>
<td>416</td>
<td>1,603</td>
<td>2008–2009</td>
<td>98</td>
<td>45</td>
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<tr>
<td>2009</td>
<td>3,228</td>
<td>752</td>
<td>∞</td>
<td>2009–2010</td>
<td>1,091</td>
<td>487</td>
<td>∞</td>
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<tr>
<td>2010</td>
<td>1,434</td>
<td>572</td>
<td>∞</td>
<td>1997–2010</td>
<td>460</td>
<td>172</td>
<td>∞</td>
</tr>
</tbody>
</table>

Harmonic \( N_e \) = 826

Generational \( N_{ve} \) = 460

Estimates are for arithmetic mean, except where indicated as harmonic mean.

N\( _e \) to \( N_{ve} \) also provides clear rational for the urgent need to increase \( N_{ve} \) for this population. These findings also may provide guidance for assessment of effects of management actions on imperiled species that are managed similarly.

**Supplementary Material**


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**Data Availability**

Data deposited at Dryad: [http://dx.doi.org/10.5061/dryad.cf730](http://dx.doi.org/10.5061/dryad.cf730)

**References**


Waples RS. 2006. A bias correction for estimates of effective population size based on linkage disequilibrium at unlinked gene loci*. *Conserv Genet*.


