Increased juvenile native fish abundance following a major flood in an Arizona river

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\textbf{ABSTRACT}

Spring floods trigger spawning in many native fishes of the desert Southwest (USA), but less is known about fish community response when native fishes are rare. Here, we document change to native and nonnative fish captures and instream habitat features following a decade-high flooding event (2019) in the Verde River (AZ) where native fish captures were rare in the years pre-flood. Using prepositioned areal electrofishing devices (PAEDs), we sampled the fish community at 90 sampling units pre-flood (2017) and resampled those same units post-flood (2019) to compare and identify changes to catch and habitat features. Relative abundance of native fishes increased from 0.6\% pre-flood (0.01 fish/PAED) to 53.0\% post-flood (1.66 fish/PAED) and was largely attributable to the presence of juvenile Roundtail Chub \textit{Gila robusta} (\textless 70 mm total length (TL)) and juvenile Sonora Sucker \textit{Catostomus insignis} (\textless 100 mm TL). Juvenile Desert Sucker \textit{Catostomus clarkii} experienced a lesser increase. One adult native fish was captured in 2017 and adult native fishes were absent from 2019 sampling. The catch of adult/subadult Common Carp \textit{Cyprinus carpio} (\textgreater 100 mm TL) declined; however, this could be related to reservoir management and not the flood. The abundance of all size-classes of Black Bass \textit{Micropterus} spp., Red Shiner \textit{Cyprinella lutrensis} and other nonnative fishes did not change. The majority (97\%) of juvenile native fishes were captured at the uppermost sampling reach. A 54\% reduction to canopy cover across all sampling reaches and an increase of fine sediments at the most downstream reach demonstrates how floods can restructure the river environment. This case-study adds evidence that protection of spring floods is vital to the persistence and recolonization of fishes native to the desert Southwest, especially where they are rare. The continued presence of nonnative species may preclude juvenile native fishes from recruiting to adults.

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Freshwater fishes native to the desert Southwest region of the United States are one of the most threatened faunal groups in North America (Rahel 2000). Of the 31 fish species native to the desert Southwest, 25 (> 80%) have experienced a significant decline or have been extirpated, and < 50% of the region’s overall fish population is composed of native fishes (Olden and Poff 2005; Schade and Bonar 2005; Turner and List 2007). Understanding the factors associated with the abundance and distribution of native and nonnative fishes serves to benefit species conservation efforts.

In general, reproduction by native fishes of the desert Southwest is driven by river discharge and annual spring freshets. A positive relationship exists between spring floods, native fish spawning activity, and juvenile recruitment (Steff erud et al. 2011). High-magnitude spring floods trigger reproduction in Roundtail Chub Gila robusta, Sonora Sucker Catostomus insignis, and Desert Sucker Catostomus clarkii, among others (Brouder 2001; Bonar and Mercado-Silva 2010). It is thought that change to the instream environment (Propst and Gido 2004), the high magnitude flows (Bestgen et al. 2011), a temperature change associated with floods (Fraser et al. 2019), or some combination of these factors motivates this response.

Rapid onset floods, characteristic of rivers of the desert Southwest, may select against nonnative fishes (Minckley and Meffe 1987; Eby et al. 2003). Nonnative fishes of this region, with origins from mesic rivers of the southeastern United States, are often evolutionarily unfit to withstand these torrents. Therefore, a reduction to the abundance of nonnative fishes has been observed in rivers of the desert Southwest immediately following major floods (Minckley and Meffe 1987; Eby et al. 2003; Rogosch et al. 2019). Because of this, rapid onset floods have been credited with some rivers’ ability to resist invasion by nonnative species. Nevertheless, some studies have observed the reduction of nonnative fishes to be transient and the nonnative fish community has returned to preflood levels rapidly (Pool and Olden 2015).

The Verde River is one of the largest remaining perennial rivers in the desert Southwest (Averitt et al. 1994). It supports a native fish community; however, populations of these fishes are severely depressed and the river is presently dominated by nonnative species (Rinne et al. 1998; Rogosch et al. 2019). In the 82 km segment of the Wild and Scenic Verde River, from Beasley Flats to Sheep Bridge, native fish capture has recently been exceptionally low. Catch from a recurring Arizona Game and Fish (AZGF) survey in the four years prior to a major flood (2015–2018) averaged 0.63 native fish/km electrofishing. Nonnative fish captures during those same surveys averaged 213.76 fish/km canoe electrofishing (Arizona Game and Fish Department (AZGF) 2015, 2018). Additionally, our own pre-flood sampling captured one native fish in ninety sampling units in 2017.

In February 2019, the Verde River experienced a flood with an instantaneous peak flow of 1,416 m$^3$/s (USGS gage 09506000; Figure 1). This was the largest flood of the decade, and the second largest flood recorded here since 2000. This flood afforded us an opportunity to examine change to fish community structure and instream habitat features.
at multiple locations within the Verde River by revisiting previously sampled sites. We asked the following research questions: Would production and recolonization of young be so low as to be virtually undetectable? Would production of young spawned from only a few fish result in the detection of native juveniles at all study reaches surveyed or only at specific locations? Would the flood redistribute instream habitat features and would that change along the river continuum? This research can benefit conservation by adding to the body of evidence that demonstrates the importance of floods to native fishes of the desert Southwest, while investigating the potential for a depauperate native fish community to seed a river with juveniles.

**Methods**

**Study site**

The Verde River flows for 274 km from its origins at Big Chino Wash (1325 masl) to its terminus at the confluence with the Salt River in central Arizona (402 masl). For the first 200 km the mainstem Verde River is free flowing, at which point it is impounded by Horseshoe Reservoir (Averitt et al. 1994; Figure 2). This unobstructed condition has allowed for the retention of a relatively natural flow regime, which is characterized by a variable and flashy hydrograph and periodic high magnitude (> 283.17 m³/s) floods (Averitt et al. 1994; Serrat-Capdevila et al. 2013). The lower ~82 km of the Verde River, prior to impoundment in Horseshoe Reservoir, is designated as Wild and Scenic (Public Law 90-542; 16 U.S.C. 1271 et seq.). Historically, twelve native fish species occupied the
Verde River (Rinne et al. 1998), of which five are extant (Roundtail Chub, Sonora Sucker, Desert Sucker, Longfin Dace *Agosia chrysogaster*, and Speckled Dace *Rhyinichthys osculus*). The present fish community is dominated by nonnative species, including Red Shiner *Cyprinella lutrensis*, Black Bass *Micropterus spp.*, Common Carp *Cyprinus carpio*, Rainbow Trout *Oncorhynchus mykiss*, Green Sunfish *Lepomis cyanellus*, Flathead Catfish *Pylodictis olivaris*, Channel Catfish *Ictalurus punctatus*, Bullhead Catfish *Ameiurus spp.*, and other members of the sunfish (Centrarchidae) and minnow (Cyprinidae) families.

**Data collection**

We sampled fish using prepositioned areal electrofishing devices (PAEDs). Prepositioned areal electrofishing devices reduce fright bias, allow for a multispecies analysis, and are useful in quantifying fish abundance as it relates to discrete microhabitat conditions (Bain...
et al. 1985; Bovee 1986). The motivation for using this sampling gear was to develop habitat models for fishes of the Verde River (Jenney 2020), but these models are beyond the scope of this current manuscript, which is focused on juvenile native fish production following a major flood. The effectiveness of PAEDs – and all electrofishing methods (Guy et al. 2009) – decreases with increased depth and is most effective in shallow and littoral areas. Therefore, we limited our sampling to shallow water \( \leq 1.5 \text{ m} \) in depth (Bowen and Freeman 1998). Prepositioned areal electrofishing devices provide a repeatable and consistent method of sampling (Ensign et al. 2002), allowing for a direct comparison between sampling events (Bain et al. 1985; Lucas and Baras 2000).

We constructed PAEDs using two steel pipes (1.5 m long, 1.3 cm diameter) that acted as an anode and cathode, separated by 1.0 m, resulting in a 1.5 m\(^2\) immobilization area. The 1.5 m\(^2\) area between the anode and cathode was considered the sampling unit. Each PAED was connected to a 15.24 m, 12-gauge extension cord that was set downstream and connected to a 2,000/1,400 Watt gasoline powered generator (Buffalo Tools, O’Fallon, Missouri). The generator supplied 120 v of alternating current (AC) to each PAED, as measured by a multimeter. We placed the PAED on the streambed with the anode and cathode positioned parallel to streamflow. We allowed the PAED to sit undisturbed for a minimum of 11 min while technicians remained onshore and distant from the PAED to limit frightening fish into or out of the sampling unit. The 11 min wait has been established as sufficient for fish to recolonize holding locations following disturbance (Bain et al. 1985; Bonar et al. 2010; Nemec et al. 2021). We then energized the sampling unit for a minimum of 15 s as a technician approached the PAED from downstream and netted immobilized fishes. We identified captured fish to species and measured fish to a TL (mm) prior to releasing the individual at, or near, their capture location.

We established three 1,000 m reaches in the Verde River, at Beasley Flats (34.47320, -111.80180), Childs River Access (34.34748, -111.69783), and Sheeps Bridge (34.07768, -111.70755), hereafter referred to as the upper, middle, and lower reaches. The upper reach was \( \approx 23 \text{ km} \) upstream of the middle reach and \( \approx 82 \text{ km} \) upstream of the lower reach. These reaches provided access into the wilderness segment of the river and allowed us to investigate change to the fish community and instream environment along the river continuum. Ninety locations, thirty at each 1,000 m reach, were sampled using the same PAEDs and techniques pre-flood in 2017 (June 27 – 30) and post-flood in 2019 (June 3–28) to obtain discrete samples of the fish community. The locations of the 90 sampling units were randomly selected in 2017 and revisited in 2019. Discharge during sampling averaged 1.27 m\(^3\)/s in 2017 and 1.70 m\(^3\)/s in 2019 (USGS Gage 09506000, \( \approx 5.6 \text{ km} \) downstream from our upper most sampling unit and \( \approx 75.3 \text{ km} \) upstream from the lower most sampling unit).

We measured total depth, flow velocity, substrate composition, and canopy cover within each sampling unit, regardless of whether fish were captured (Bovee 1986; Bonar et al. 2010). Methods used to collect habitat data were identical in 2017 and 2019. We measured total depth, and flow velocity at 60% of total depth, in each corner of the PAED using a wading rod with an electromagnetic current meter (Hach, Loveland, Colorado). The four measurements were then averaged to calculate a mean depth and flow velocity for each sampling unit. We categorized substrate according to the modified Wentworth scale (Bain 1999; Boulder >265 mm in diameter; cobble = 64 – 256 mm; pebble = 16 – 63 mm; gravel = 2 – 15 mm; sand = 0.06 – 1.00 mm; silt < 0.059 mm). We randomly placed a 1 m chain with markings every 10 cm within each 1.5 m\(^2\) sampling unit and categorized substrate at each demarcation. We calculated the mode of these ten categorizations to determine the dominant substrate within each sampling unit. We estimated
overhead canopy cover using a spherical densiometer, as described in Lemmon (1956). Each densiometer had twenty-four square cells etched onto its surface. We counted the cells that had vegetation present in at least 3/4 of its area and divided that number by the total number of cells to calculate the proportion of overhead canopy cover. We measured canopy cover in four directions, upstream, downstream, towards the right bank, and towards the left bank, and averaged the measurements.

**Data analysis**

Fish were analyzed by size class. We defined juvenile Roundtail Chub as fish ≤ 70 mm TL and subadult/adult fish (hereafter, referred to as adult fish) as Roundtail Chub > 70 mm TL (Brouder 2001). All other fishes were classified as juveniles if ≤ 100 mm TL, and adults if > 100 mm TL, based upon methods described in previous research (Rees et al. 2005; Pilger et al. 2010). Red Shiner were analyzed as a single adult grouping. We grouped Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *Micropterus dolomieu*, and Redeye Bass *Micropterus coosae* as one species complex, Black Bass. A concurrent study found that these bass species readily hybridize within the Verde River (Jenney and Peatman 2019, unpublished report), complicating field identification.

To compare catch from 2017 pre-flood sampling to 2019 post-flood sampling, we calculated a relative abundance and a mean catch per PAED for each species and size-class. Count data was nonnormal with an unequal variance, thus violating the assumptions of the paired *T*-test. Therefore, we used a nonparametric Wilcoxon signed-rank test to test the null hypothesis that there was no difference in mean catch per PAED between the 2017 and 2019 sampling years. This test discards zero-difference values and rank transforms the differences that remain. We also used a simulated permutation test for paired data to validate the results of the Wilcoxon signed-rank test. We tested the null hypothesis that either of the two values of the paired data were equally as likely, and therefore, the sign of the difference (positive or negative) could be reversed without consequence. We then computed a *T*-statistic for each permuted sample to approximate the distribution of the *T*-statistic from 100,000 iterations of this test (Eudey et al. 2010). The simulated permutation test provided a reasonable approximation of *P*-values to validate the *P*-values derived from the nonparametric test.

We investigated change to habitat features using a series of *T*-tests where appropriate and Wilcoxon signed-rank tests when the assumptions of a *T*-test were violated. To investigate change to depth and overhead cover, we tested the null hypothesis that the mean values for each habitat feature were not different between sampling years using paired *T*-tests. Depth was nonnormally distributed, and therefore, we applied a log-transformation prior to analysis. Though overhead canopy cover was proportional, it was normally distributed and treated as a continuous variable for this paired analysis. Flow velocity and substrate composition were analyzed with a Wilcoxon signed-rank test due to flow velocity being nonnormally distributed and substrate composition being categorical. Additionally, we assigned a numeric code (Bain 1999; 5 = boulder, 4 = cobble, 3 = pebble, 2 = gravel, 1 = sand, 0 = silt) to each sampling unit based on the dominant substrate present. We then calculated a mean of the substrate codes at the sampling reach and overall study-reach. This method is inappropriate for identifying a specific substrate-type but is useful to document a mean change to substrate between sampling years. All statistical analyses were completed using the program R version 3.6.1 (R Core Team 2017).
Results

Fish abundance

We captured a total of 441 fish of 9 species (3 native and 6 nonnative). In 2017, we captured zero fish at 51% (46 of 90 PAEDs) of all sampling units and in 2019 we captured zero fish at 44% (40 of 90 PAEDs) of all sampling units. Species richness increased from 2017 ($n = 7$) to 2019 ($n = 9$) due to the appearance of two native species, Roundtail Chub and Sonora Sucker. Additionally, the relative abundance of native fishes increased from 0.6% of the total catch in 2017 to 53% of the total catch in 2019.

The increase in native fishes ($P = 0.003$) was due to the increased capture of juvenile fishes (Table 1). Juvenile native fishes were absent in 2017, but in 2019, catch of juvenile native fishes was 0.29 fish/PAED; 1.32 fish/PAED for Roundtail Chub ($P = 0.003$); Sonora Sucker ($P = 0.027$) and Desert Sucker ($P = 0.317$), respectively. Despite this increase, juvenile Roundtail Chub were absent from 88% of sampling units, juvenile Sonora Sucker were absent from 94% of sampling units, and Desert Sucker were absent from 98% of sampling units in 2019. Additionally, 80 of the 119 juvenile Sonora Sucker were captured in a single sampling unit within the upper reach. We captured one adult native fish, a Desert Sucker, in 2017. No other adult native fishes of any species were captured during sampling. Ninety-seven percent of all native fishes were captured at the upper reach (4.80 fish/PAED, SE = 1.696). The remaining 3% of native fishes were captured at the lower reach (0.17 fish/PAED, SE = 0.049). No native fishes were captured at the middle reach in either year.

Captures of nonnative fishes was not significantly different between sampling years ($P = 0.994$). Captures of juvenile Common Carp ($P = 0.198$), Black Bass ($P = 0.549$), Green Sunfish ($P = 0.317$), and Flathead Catfish ($P = 0.317$) remained similar. Similarly, captures of adult Black Bass ($P = 0.706$), Red Shiner ($P = 0.235$), Green Sunfish ($P = 1.00$),

| Table 1. Total captures and standard error for fish captured throughout the two-year study period reported in this study. |
|-----------------------------------------------|
| Species | Size Class | Total Captures | Standard Error | Z-score | P-value | Pperm-value |
|---------|------------|----------------|----------------|---------|---------|-------------|
| Roundtail Chub* | J | 0 | 26 | 0.00 | 0.12 | 2.990 | 0.003 | 0.001 |
| Roundtail Chub* | A | 0 | 0 | 0.00 | 0.00 | – | – | – |
| Sonora Sucker* | J | 0 | 119 | 0.00 | 0.97 | 2.210 | 0.027 | 0.032 |
| Sonora Sucker* | A | 0 | 0 | 0.00 | 0.00 | – | – | – |
| Desert Sucker* | J | 0 | 4 | 0.00 | 0.04 | 1.000 | 0.317 | 1.000 |
| Desert Sucker* | A | 1 | 0 | 0.01 | 0.00 | –1.000 | 0.317 | 1.000 |
| Black Bass | J | 21 | 26 | 0.08 | 0.07 | 0.599 | 0.549 | 0.683 |
| Black Bass | A | 4 | 5 | 0.02 | 0.03 | 0.378 | 0.706 | 1.000 |
| Common Carp | J | 5 | 1 | 0.04 | 0.01 | –1.290 | 0.198 | 0.377 |
| Common Carp | A | 42 | 4 | 0.14 | 0.02 | –3.220 | 0.001 | 0.001 |
| Red Shiner | A | 80 | 88 | 0.33 | 0.27 | 1.190 | 0.235 | 0.869 |
| Green Sunfish | J | 0 | 1 | 0.00 | 0.01 | 1.000 | 0.317 | 1.000 |
| Green Sunfish | A | 1 | 1 | 0.01 | 0.01 | 1.000 | 0.317 | 1.000 |
| Flathead Catfish | J | 0 | 1 | 0.00 | 0.01 | 1.000 | 0.317 | 1.000 |
| Flathead Catfish | A | 4 | 4 | 0.02 | 0.02 | 0.333 | 0.739 | 1.000 |
| Channel Catfish | J | 0 | 0 | 0.00 | 0.00 | – | – | – |
| Channel Catfish | A | 2 | 1 | 0.02 | 0.01 | –0.577 | 0.564 | 1.000 |
| Native* | All | 1 | 149 | 0.01 | 1.00 | 2.990 | 0.003 | 0.001 |
| Nonnative | All | 159 | 132 | 0.38 | 0.30 | –0.008 | 0.994 | 0.529 |

Data from 2017 represents pre-flood captures and data from 2019 represents post-flood captures. Size class denotes whether the fish was a juvenile ($J; \leq 100 \text{ mm TL}$) or an adult/subadult ($A; > 100 \text{ mm TL}$); however, Roundtail Chub were classified as juvenile if $< 70 \text{ mm TL}$ and a subadult/adult if $> 70 \text{ mm TL}$. The Z-Score and P-value are from a nonparametric Wilcoxon signed-rank test. $P_{perm}$-value is the $P$-value derived from a simulated permutation test for paired data (100,000 iterations), used to validate results from the nonparametric tests of symmetry. * represents a native species.
Flathead Catfish ($P = 0.739$), and Channel Catfish ($P = 0.564$) we’re not significantly different (Table 1). The abundance of adult Common Carp declined from 0.47 fish/PAED in 2017 to 0.04 fish/PAED in 2019 ($P = 0.001$). All captures of adult Common Carp occurred at the lower reach in 2017; however, Common Carp were present at all three reaches in 2019.

**Habitat availability and distribution**

We found no difference in the distribution of habitat features depth ($P = 0.494$), flow velocity ($P = 0.464$), or substrate composition ($P = 0.859$) at the overall study-scale; however, the mean depth increased at the upper reach ($P = 0.043$), the mean flow velocity decreased at the lower reach ($P = 0.049$), and the mean substrate size increased at the upper reach ($P = 0.017$) and decreased at the lower reach ($P = 0.037$; Table 2). Canopy cover was reduced by 65% at the upper reach ($P < 0.001$) and nearly 80% at the lower reach ($P < 0.001$), resulting in a reduction of > 50% at the overall study-reach ($P < 0.001$).

**Discussion**

Our observations, combined with conclusions from past research (Craven et al. 2010; Stefferud et al. 2011), suggest that the observed increase to the abundance of juvenile native fishes was due to spawning triggered by the flood of February 2019. First, floods
and native fish reproductive success has been linked for many native fishes of the desert Southwest (Tyus and Karp 1989; Minckley and Marsh 2009). No juvenile fish were captured in our 2017 survey or other surveys of the river in the four previous years (Arizona Game and Fish Department (AZGF) 2015, 2018) when no major floods occurred. Second, no other large-scale event besides the flood of 2019 occurred between the two-years to trigger spawning on this scale. It should be noted that the flow magnitude required to trigger reproduction is unknown; however, Brouder (2001) found that the CPUE of age-1 Roundtail Chub increased linearly as a function of flow magnitude one-year after a flood.

Following the flood of 2019, juvenile native fishes were abundant relative to previous years, suggesting that a few individuals can seed a river if high magnitude spring flooding occurs. The reseeding we saw was patchy, with most juvenile native juvenile fishes being captured at the upper reach. Juveniles were present at the lowermost site, albeit in low abundance. Sampling reported in this study focused on 90 sampling units surveyed before and after a flood in a paired design. However, we sampled 292 additional sampling units in 2019 which were not included in the analysis presented in this manuscript as they did not share locations with pre-flood sampling units. These efforts resulted in the capture of an additional 263 juvenile Roundtail Chub, 53 juvenile Sonora Sucker, and 34 juvenile Desert Sucker in the ~24 km segment of river between the upper and middle reaches reported in this study. An AZGF monitoring program, which surveyed this same ~24 km segment, captured one adult native fish in both 2015 and 2018, and juvenile native fishes were not present (Arizona Game and Fish Department (AZGF) 2015, 2018). This provides further evidence that juvenile fish production was related to the flood of 2019. Our findings combined with past research (Brouder 2001; Rinne et al. 2004; Stefferud et al. 2011) suggests that, given spring flooding, small numbers of native fishes can naturally reproduce and repopulate a stream. Furthermore, evidence suggests that the production of young fishes resulted from mainstem spawning and not that in tributaries because the largest concentration of juveniles was distant and upstream from major tributaries, native fishes of the desert Southwest have adaptations limiting displacement from natal streams by major flooding (Minckley and Meffe 1987), and the capture of a single ‘ripe’ adult Roundtail Chub during a concurrent sampling event provides evidence of the spawning potential within the mainstem Verde River (Jenney 2020).

Although juveniles were produced following the flood of 2019, recruitment is uncertain (Steff erud et al. 2011). To that point, an AZGF survey that occurred two years post-flood (2021) encountered only two native fish, one adult Roundtail Chub and one adult Sonora Sucker (relative abundance = 0.28%; personal communication, AZGF, 2021). Predation by nonnative fishes is the primary reason that native fishes of the desert Southwest fail to recruit (Clarkson et al. 2005; Gibson et al. 2015). This is likely the case on the Verde River, as well (Rinne et al. 1998; Rinne and Miller 2006). The continued lack of native fishes of any size-class two years after a large influx of juveniles likely indicates that recruitment is poor and that floods alone are insufficient to recover native fishes.

The differential response observed along the river continuum and among native fishes may be due to species’ susceptibility to predation (Clarkson et al. 2005), their ability to cope with habitat alterations (Gibson et al. 2015), and their pre-flood abundance and distribution (Rinne et al. 1998). Ninety-seven percent of all native fishes were captured at the upper reach. No native fishes of any size-class were captured at the middle reach, and the remaining 3% were captured at the downstream reach. This might suggest that lower in the river, populations of native fishes are too small to reproduce in any meaningful numbers, nonnative fishes are abundant and depredate young fishes that are produced, or a combination of both. Our findings are consistent with previous research that found native
fishes to be concentrated in upstream locations (Rinne et al. 1998). More pool-like habitat due to a lessening gradient occurs downstream (Franssen et al. 2016) and these environments likely favor nonnative fishes present in the Verde River (Gibson et al. 2015).

The use of PAEDs allowed for consistent and easily repeatable sampling (Bowen and Freeman 1998; Ensign et al. 2002), which facilitated a direct comparison of the fish community between sampling years. However, the use of PAEDs could have resulted in an underestimation of the abundance of fishes inhabiting depths > 1.5 m. This would not invalidate our overall conclusions, as juvenile fishes are known to inhabit shallow-water habitats and littoral zones (Travnichek et al. 1995; Baras and Nindaba 1999) within our sampling frame. Furthermore, the utility and efficiency of PAEDs increases when they are used to quantify juvenile fish abundance (Freeman et al. 2001). Prepositioned areal electrofishing devices have been used successfully to evaluated species richness (Branigan et al. 2018), fish density, and the relative abundance of fishes inhabiting shallow-water lotic environments (Travnichek et al. 1995).

Multiple studies have found that Roundtail Chub, Sonora Sucker, and Desert Sucker spawn on the receding limb of the hydrograph following floods. This life-history strategy would enable native fishes to synchronize spawning to periods when spawning habitats, specifically clean gravel substrates in riffles, are maximized (Lytle and Poff 2004; Propst and Gido 2004). Our research, finding a reduction to substrate size at the most downstream sampling location, supports this hypothesis. Additionally, the significant reduction to overhead canopy cover provides evidence that high magnitude floods in the desert Southwest can restructure the river environment. Yet, previous research found no relationship between change to microhabitat characteristics and juvenile fish year-classes (Strange et al. 1993), which may suggest that native fishes are responding to the flow itself, the temperature change associated with such flows (Fraser et al. 2019), or a combination of both, and not to the distribution of habitat features.

Evidence exists of high-magnitude floods selecting against nonnative fishes within the desert Southwest (Minckley and Meffe 1987; Rinne 1994; Whitney et al. 2014). Consistent with these findings, catch of Common Carp, a fish adapted to low flow velocity environments (Butler and Wahl 2010), declined from 2017 to 2019. A similar reduction to Common Carp was observed in Aravaipa Creek, AZ following major flooding (Minckley and Meffe 1987). Alternatively, the annual drawdown of the downstream Horseshoe Reservoir, which occurred prior to sampling in 2017, may have forced Common Carp into the mainstem Verde River, resulting in increased catch. All Common Carp captures from 2017 occurred at the lower reach, closest to the reservoir. In 2019, the drawdown of Horseshoe Reservoir occurred after sampling (Wicke 2020). Common Carp would have had ample space within the reservoir and might not have been forced into the river environment, thus limiting instream captures. The abundance of all other nonnative fishes remained stable between sampling years, suggesting that the flood had no measurable impact on these species (Rinne 1994; Olden and Poff 2005). Species including Black Bass and Red Shiner are tolerant of elevated flow velocities and possess morphological and behavioral pre-adaptations – a fusiform body shape, an ability to withstand elevated flow velocities, a tolerance for rapid changes to water quality – that likely increased these species’ resistance to floods (Edwards et al. 1983; Ward et al. 2003). The reduction to nonnative fishes reported in previous research (Minckley and Meffe 1987) may be exclusive to canyon-bound reaches of small streams where refuge from disruptive flows is sparse (Propst et al. 2008; Ruhi et al. 2016). Our findings are consistent with research from larger rivers within the desert Southwest where the nonnative fish community returned to a preflood level within 8 days of a large flood (Pool and Olden 2015).
Our case study supports research showing the importance of spring floods to native fish production in the desert Southwest. It demonstrates that few fish can seed large numbers of juveniles, though recruitment is uncertain. The failure of large-scale floods to remove nonnative species suggests reducing populations of nonnative fishes by other means, in addition to maintaining spring floods, is important for native fish recruitment (Tyus and Saunders 2000). Past conservation efforts have largely focused on maintaining a minimum baseflow (Neary and Rinne 1998), clearly needed for the survival of fishes. However, a growing body of evidence emphasizes the importance of other flow components (Poff 2018), such as periodic high magnitude floods. Efforts to harvest flood-flow, in addition to baseflow, may interfere with native fish spawning and the reseeding of streams unless the importance of floods is considered.

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Disclosure statement

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Data availability

Data used in this study can be found at the following link. https://osf.io/tkrvj/?view_only=5fadfeccbeb85248af9e87371992215a23
References

Arizona Game and Fish Department (AZGF). 2015. Verde river: Beasley flats – Childs Fish Survey Report June 2015, Region III fisheries program. Phoenix (AZ): Arizona Game and Fish Department.

Arizona Game and Fish Department (AZGF). 2018. Verde river: Beasley Flats – Childs Fish Survey Report July 2018, Region III fisheries program. Phoenix (AZ): Arizona Game and Fish Department.

Arizona General Stream Adjudication Bulletin (AZGSAB). 2018. Aravaipa Canyon Wilderness Area, Contested Case No. W1-11-3342. Vol. 26, No. 3, 17 December 2018.

Averitt E, Steiner F, Yabes RA, Patten D. 1994. An assessment of the Verde River corridor project in Arizona. Landscape Urban Plann. 28(2–3):161–178.

Bain MB. 1999. Substrate. In: Bain MB, Stevenson NJ, editors. Aquatic habitat assessment: Common methods. Bethesda (MD): American Fisheries Society; p. 95–103.

Bain MB, Finn JT, Booke HE. 1985. A quantitative method for sampling riverine microhabitats by electrofishing. North Am J Fish Manage. 5(3b):489–493.

Baras E, Nindaba J. 1999. Seasonal and diel utilization of inshore microhabitats by larvae and juveniles of Leuciscus cephalus and Leuciscus leuciscus. Environ Biol Fishes. 56(1–2):183–197.

Bestgen KR, Haines GB, Hill AA. 2011. Synthesis of flood plain wetland information: timing of Razorback Sucker reproduction in the Green River, Utah, related to stream flow, water temperature, and flood plain wetland availability. Fort Collins, Colorado: Colorado State University, Larval Fish Laboratory Contribution 163.

Bonar SA, Mercado-Silva N, Rogowski D. 2010. Habitat use by the fishes of a southwestern desert stream: Cherry Creek, Arizona. Arizona Cooperative Fish and Wildlife Research Unit, Fisheries Research Report 02-10, Tucson.

Bonar SA, Mercado-Silva N. 2010. Aravaipa Canyon Wilderness Area (w1-11-3342), in the general adjudication of all rights to use water in the Gila River System and source, Ariz. Sup. Ct. Case Nos. W1-W4. Environmental and Natural Resources Division. U.S. Department of Justice.

Bovee KD. 1986. Development and evaluation of habitat suitability criteria for use in the instream flow methodological U.S. Fish and Wildlife Service, Biological Report 86. p. 7. Washington, DC.

Bown ZH, Freeman MC. 1998. Sampling effort and estimates of species richness based on prepositioned area electoﬁsher samples. North Am J Fish Manage. 18(1):144–153.

Branigan PR, Quist MC, Shepard BB, Ireland SC. 2018. Comparison of a prepositioned area electrofishing device and ﬁxed underwater videography for sampling riverine fishes. Western North Am Naturalist. 78(1):65–75.

Brouder MJ. 2001. Effects of flooding on recruitment of Roundtail Chub, Gila robusta, in a Southwestern River. Southwestern Natural. 46(3):3: 302–310.

Butler SE, Wahl DH. 2010. Common Carp distribution, movements, and habitat use in a river impounded by multiple low-head dams. Trans Am Fish Soc. 139(4):1121–1135.

Clarkson RW, Marsh PC, Stefferud SE, Stefferud JA. 2005. Conﬂicts between native fish and nonnative sport ﬁsh management in the southwestern United States. Fisheries. 30(9):20–27.2.0.CO;2

Craven SW, Peterson JT, Freeman MC, Kwak TJ, Irwin E. 2010. Modeling the relations between ﬂow regime components, species traits, and spawning success of fishes in warmwater streams. Environ Manage. 46(2):181–194.

Eby LA, Fagan WF, Minkley WL. 2003. Variability and dynamics of a desert stream community. Ecol Appl. 13(6):1566–1579.

Edwards EA, Gebhart G, Maughan OE. 1983. Habitat suitability information: Smallmouth bass. U.S. Dept. Int., Fish Wildl. Serv. FWS/OBS-82/10.36.

Ensignment WE, Temple AJ, Neves RJ. 2002. Effects of fright bias on sampling efﬁciency of stream ﬁsh assemblages. J Freshwater Ecol. 17(1):127–139.

Eudey TL, Kerr JD, Trumbo BE. 2010. Using R to simulate permutation distributions for some elementary experimental designs. J Statist Educ. 18(1):1–30.

Franssen NR, Durst SL, Gido KB, Ryden DW, Lamarrava V, Propst DL. 2016. Long-term dynamics if large-bodied fishes assessed from spatially intensive monitoring of a managed desert river. River Res Appl. 32(3):348–362.

Fraser GS, Bestgen KR, Winkelman DL, Thompson KG. 2019. Temperature- not ﬂow-predicts native ﬁsh reproduction with implications for climate change. Trans Am Fish Soc. 148(3):509–527.

Freeman MC, Bowen ZH, Bovee KD, Irwin ER. 2001. Flow and habitat effects on juvenile ﬁsh abundance in natural and altered ﬂow regimes. Ecol Appl. 11(1):179–190.2.0.CO;2

Gibson PP, Olden JD, O’Neill MW. 2015. Beaver dams shift desert ﬁsh assemblages toward dominance by non-native species (Verde River, Arizona, USA). Ecol Freshw Fish. 24(3):355–372.
Guy CS, Braaten RJ, Herzog DP, Pitlo J, Rogers RS. 2009. Warmwater fish in rivers. In: Bonar SA, Hubert WA, Willis DW, editors. Standard methods for sampling north american freshwater fishes, Bethesda (MD): American Fisheries Society; pp. 59–84.

Jenney CJ. 2020. Assessing pre- and post-flood fish abundance, population structure, and habitat use in an Arizona river (Document No. 28260830) [Master’s thesis]. Tucson (AR): ProQuest Dissertations Publishing. [University of Arizona]

Jenney, C, Peatman E. 2019. Verde River black bass genetics. Unpublished manuscript.

Lemmon PE. 1956. A spherical densiometer for estimating forest overstory density. Forest Sci. 2(4): 314–320.

Lucas MC, Baras E. 2000. Methods for studying spatial behavior of freshwater fishes in the natural environment. Fish Fisheries. 1(4):283–316.

Lytle DA, Poff NL. 2004. Adaptation to natural flow regimes. Trends Ecol Evol. 19(2):94–100.

Minckley WL, Marsh PC. 2009. Inland fishes of the greater southwest: Chronicle of a vanishing biota. Tucson (AR): The University of Arizona Press.

Minckley WL, Meffe GK. 1987. Differential selection by flooding in stream-fish communities of the arid American Southwest. In Matthews WJ, Heins DC, editor. Community and evolutionary ecology of North American stream fishes. Norman (OK): University of Oklahoma Press, p. 93–104.

Neary DG, Rinne JN. 1998. Baseflow trends in the upper Verde River relative to fish habitat requirements. Hydrol Water Resource Arizona Southwest. 27:57–64.

Nemec ZC, Lee LN, Bonar SA. 2021. Development and evaluation of habitat suitability criteria for native fishes in three Arizona streams. North Am J Fish Manage. 41(3):661–677.

Olden JD, Poff NL. 2005. Long-term trends of native and non-native fish faunas in the American Southwest. Anim Biodivers Conserv. 28:75–89.

Piilger TJ, Gido KB, Propst DL. 2010. Diet and trophic niche overlap of native and nonnative fishes in the Gila River, USA: implications for native fish conservation. Ecol Freshwater Fish. 19(2):300–321.

Poff NL. 2018. Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world. Freshw Biol. 63(8):1011–2021.

Pool TK, Olden JD. 2015. Assessing long-term fish responses and short-term solutions to flow regulation in a dryland river basin. Ecol Freshw Fish. 24(1):56–66.

Propst DL, Gido KB, Stefferud JA. 2008. Natural flow regimes, nonnative fishes, and native fish persistence in arid-land river systems. Ecol Appl. 18(5):1236–1252.

Propst DL, Gido KB. 2004. Responses of native and nonnative fishes to natural flow regime mimicry in the San Juan River. Trans Am Fish Soc. 133(4):922–931.

R Core Team. 2017. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. https://www.R-project.org/.

Rahel FJ. 2000. Homogenization of fish faunas across the United States. Science. 288(5467):854–856.

Rees DE, Ptacek JA, Miller WJ. 2005. Roundtail Chub (Gila robusta robusta): A technical conservation assessment. USGS Forest Service, Species Conservation Project. Fort Collins, Colorado.

Rinne, JN, Miller D. 2006. Geomorphology and management: implications for sustainability of native Southwestern fishes. Reviews in Fisheries Science. 14(1): 91–110.

Rinne JN, Riley L, Bettaso R, Sorenson R, Young K. 2004. Managing southwestern native and nonnative fishes. Can we mix oil and water and expect a favorable solution? Am Fish Soc Sympos. 44:445–466.

Rinne JN, Stefferud JA, Clark A, Sponholtz P. 1998. Fish community structure in the Verde River, Arizona, 1974-1997. Hydrol Water Resource Arizona Southwest. 28:75–80.

Rinne JN. 1994. Declining southwestern aquatic habitats and fishes: are they sustainable? In Flagstaff A, Covington WW, DeBano LF, Technical Coordinators. Sustainable ecological systems: implementing an ecological approach to land management, Gen. Tech. Rep. RM-247, July 1993; p. 12–15.

Rogosch JS, Tonkin JD, Lytle DA, Merritt DM, Reynolds LV, Olden JD. 2019. Increasing drought favors nonnative fishes in a dryland river: evidence from a multispecies demographic model. Ecosphere. 10(4):1–19.

Ruhi A, Olden JD, Sabo JL. 2016. Declining streamflow induces collapse and replacement of native fish in the American Southwest. Front Ecol Environ. 14(9):465–472.

Schade CB, Bonar SA. 2005. Distribution and abundance of nonnative fishes in streams of the western United States. North Am J Fish Manage. 25(4):1386–1394.

Serrat-Capdevila A, Valdes JB, Dominguez F, Rajagopal S. 2013. Characterizing the water extremes of the new century in the US Southwest: a comprehensive assessment from state-of-the-art climate model projections. Int J Water Resour Dev. 29(2):152–171.

Stefferud JA, Gido KB, Propst DL. 2011. Spatially variable response of native fish assemblages to discharge, predators, and habitat characteristics in an arid-land river. Freshwater Biol. 56(7):1403–1416.
Strange EM, Moyle PB, Foin TC. 1993. Interactions between stochastic and deterministic processes in stream fish community assembly. Environ Biol Fish. 36(1):1–15.

Travnichek VH, Bain MB, Maceina MJ. 1995. Recovery of a warmwater fish assemblage after the initiation of a minimum-flow release downstream from a hydroelectric dam. Trans Am Fish Soc. 124(6):836–844.

Turner DS, List MD. 2007. Habitat mapping and conservation analysis to identify critical streams for Arizona’s native fish. Aquat Conserv Mar Freshwater Ecosyst. 17:727–748.

Tyus HM, Karp CA. 1989. Habitat use and streamflow needs of rare and endangered fishes, Yampa River, Colorado. U.S. Fish and Wildlife Service, Biological Report 89. p. 14.

Tyus HM, Saunders JF. III. 2000. Nonnative fish control and endangered fish recovery: lessons from the Colorado River. Fisheries. 25(9):17–24.

Ward DL, Schultz AA, Matson PG. 2003. Differences in swimming ability and behavior in response to high water velocities among native and nonnative fishes. Environ Biol Fishes. 68(1):87–92.

Whitney JE, Gido KB, Propst DL. 2014. Factors associated with the success of native and nonnative species in an unfragmented arid land riverscape. Can J Fish Aquat Sci. 71(8):1134–1145.

Wicke MW. 2020. Horseshoe and bartlett reservoirs habitat conservation plan annual report 2020. Salt River Project, Phoenix (AR): Environmental Services and Sustainability.