

# Dynamics of a Warmwater-Coldwater Fish Assemblage in a Wildfire-Prone Landscape



David L. Propst , Dustin J. Myers, Jill M. Wick, and Ryder J. Paggen

**Abstract** Gila trout *Oncorhynchus gilae* historically occupied high-elevation (>2000 m) headwater streams of the Gila River in southwest New Mexico and central Arizona, USA. By the mid-twentieth century, human activities such as resource extraction and nonnative species introductions caused habitat degradation and loss, thereby restricting the trout to a few small remote streams in the upper Gila River catchment in New Mexico. Since 1989, conservation efforts have been hampered by numerous wildfires that caused elimination of some populations and greatly reduced others. But wildfires also eliminated nonnative fishes from streams thereby making them available for Gila trout repatriation. Elimination of all fishes, including nonnative trout, from upper Black Canyon (ca. 17 km), an East Fork Gila River tributary, by wildfire and associated sediment-laden flows in 1995 and subsequent colonization by native warmwater species (longfin dace *Agosia chrysogaster*, speckled dace *Rhinichthys osculus*, Sonora sucker *Catostomus insignis*, and desert sucker *Pantosteus clarkii*) provided the opportunity to study the dynamics of a mixed warm-coldwater fish assemblage. Although upper Black Canyon was thermally compromised (summer maxima >25 °C), age-0 hatchery-produced Gila trout (≈1000–2000) were released annually from 1998 through 2012. Establishment of a nonnative piscivore, brown trout *Salmo trutta*, added complexity to the study. By 2012, native warmwater species had thriving populations but despite limited reproduction annual stocking of Gila trout likely enabled it to persist in the stream. It was not possible to determine the effects of brown trout predation on the Gila trout

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J. Lobon-Cervia et al. (eds.), *Advances in the Ecology of Stream-Dwelling Salmonids*, Fish & Fisheries Series 44,  
[https://doi.org/10.1007/978-3-031-44389-3\\_27](https://doi.org/10.1007/978-3-031-44389-3_27)

population or negative interactions, if any, between native warmwater fishes and Gila trout. Regardless, warmwater fish and brown trout abundance was greatest in downstream reaches and that of Gila trout was greatest in the most upstream reach. Inter-annual differences in somatic metrics (condition and size structure) of the Black Canyon Gila trout population were as great as it were between it and reference populations. Unassisted re-population of upper Black Canyon by native warmwater species succinctly illustrated the importance connectivity within a drainage and the rapidity in which this was accomplished is testimony to the resilience of each species to major disturbance. In 2013, wildfire again eliminated all fishes from upper Black Canyon. Hatchery-produced Gila trout were annually stocked from 2013 through 2018 and sampling in 2018 yielded a large number of age-0 fish, suggesting that a Gila trout population might be established in upper Black Canyon, but in the absence of native warmwater fishes and piscivorous brown trout.

**Keywords** Mixed fish assemblages · *Oncorhynchus gilae* · Condition factor · Size structure · Catastrophic disturbance · Wildfire · Nonnative trout · Assisted repatriation · Conservation

## 1 Introduction

Gila trout *Oncorhynchus gilae* historically inhabited high elevation tributaries of the Gila River in southwestern New Mexico and central Arizona, USA (Fig. 1). By the late nineteenth century, extensive European settlement and accompanying habitat alteration caused by widespread domestic livestock overgrazing, timber harvest, and mineral extraction had rapidly reduced its occurrence to remote, small, upland streams. Its persistence was additionally challenged by extensive introduction of nonnative salmonids, especially rainbow trout *O. mykiss* and brown trout *Salmo trutta*. When concerted conservation efforts for the species began in the last quarter of the twentieth century, Gila trout occurred in only five small, isolated streams, all within federally managed lands (Propst et al. 2020).

Initially, the overarching conservation strategy for Gila trout was to secure occupied habitats and replicate each remnant population in other suitable streams. Securing a population typically involved ensuring it was not exposed to nonnative trout invasion by constructed or natural fish movement barriers and closing it to recreational angling. Because each remnant population was genetically distinct (Turner et al. this volume), multiple replicates of each strain were deemed essential to achieve genetic as well as demographic security. Initially, this approach appeared successful in that within about 10 years, each remnant population had at least one replicate. The efficacy of this approach was tested with the elimination of Gila trout from Diamond Creek, the species type locality, by wildfire in 1989 (Propst et al. 1992). Subsequent fires in the mid-1990s and elimination of several Gila trout populations further challenged the merits of Gila trout conservation in small



**Fig. 1** Gila Trout, *Oncorhynchus gilae*. Photo by DJ Myers

single-strand headwater streams (Brown et al. 2001). Consequently, conservation strategies shifted to establishing Gila trout populations in large, dendritically complex drainages in the belief that such systems would be sufficiently large that if wildfire burned in the catchment Gila trout would have refuge in unburned portions and individuals from unaffected reaches could colonize reaches depopulated by the effects of wildfire.

As conservation strategies for Gila trout were evolving in the 1990s to ameliorate the risk posed by wildfires, empirical and theoretical evidence for climate change, in particular global warming, was rapidly accumulating and model projections for the American Southwest, and the entire Gila River drainage, were particularly dire (Williams et al. 2020). Collectively, these models projected increasing temperatures, increasing aridity, shifting precipitation patterns (including increased frequency of extreme events), diminishment and loss of snowpack, and altered stream flow regimes (Gutzler 2013; Dettinger et al. 2015; Udall and Overpeck 2017). The net effect of climate change would be substantially less optimal habitat for trout, but also an increase in wildfire frequency, extent, intensity, and severity (Westerling et al. 2006).

In a region having comparatively few perennial streams, even at higher elevations, and these are generally disconnected, persistence of robust trout populations is problematic even under current climatic conditions. Optimal habitat for Gila trout is limited and generally occurs  $\geq 2000$  m. Under conditions projected by climate models, the lower elevational limits of optimal habitat will increase (Kennedy et al. 2008). The contraction of optimal habitat will be driven mainly by elevated thermal

regimes and diminished and altered flow regimes. With these changes, lower reaches of traditional Gila trout habitat will become inhabitable by warmwater species. Survival of Gila trout might therefore ultimately depend on whether it can coexist with warmwater species in thermally sub-optimal trout habitat.

## 2 Setting

In 1995, wildfire induced ash- and sediment-laden flows eliminated nonnative trout and native fishes (cyprinids and catostomids) from upper reaches of Black Canyon, a Gila River tributary in southwest New Mexico (Fig. 2). Over the next 2 years, native cyprinids and catostomids from downstream refugia colonized depopulated stream reaches but nonnative trout did not. In June 1998, a fish movement barrier was constructed to preclude return of nonnative salmonids to the upper-most 17 km of Black Canyon and release of hatchery-reared native Gila trout was planned for that autumn. After barrier construction, a final check of Black Canyon was made to ensure absence of nonnative trout; four brown trout and one rainbow trout were found at a single location. Because rainbow trout hybridize with Gila trout and brown trout prey upon and compete with Gila trout their presence was untenable. Surrendering Black Canyon to nonnative trout was not an option. The presence of

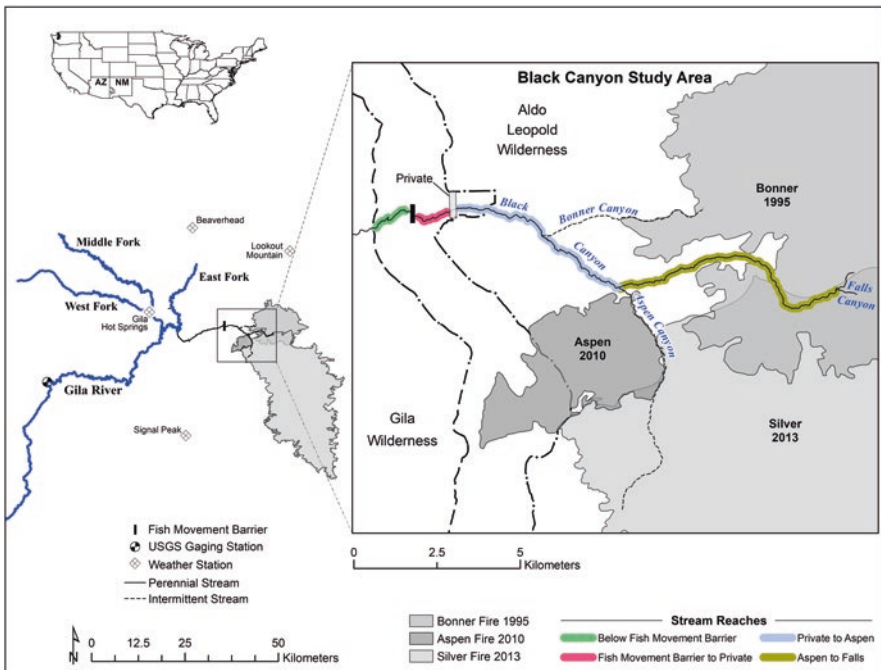


Fig. 2 Black Canyon, New Mexico study area

viable populations of four native warmwater species (longfin dace *Agosia chryso-gaster*, speckled dace *Rhinichthys osculus*, Sonora sucker *Catostomus insignis*, and desert sucker *Pantosteus clarkii*) precluded use of piscicides to eliminate nonnative trout. The alternative was mechanical removal of nonnative trout with electrofishing gear. From June through October 1998, Black Canyon was electro-fished on multiple occasions with multiple crews to capture nonnative trout (Brooks and Propst 1999). In addition to brown trout and rainbow trout, seven cutthroat trout *Oncorhynchus clarkii* individuals were collected. All brown trout collected ( $n = 345$ ) were of a single cohort (age 1) and evidently of hatchery origin as scale circuli were evenly spaced, all rainbow trout ( $n = 24$ ) were sub-adults or adults ( $>170$  mm total length), and cutthroat trout were all adults ( $>250$  mm total length). The likely provenance of brown trout, absence of age-0 rainbow trout, and first record of cutthroat trout strongly suggested their illegal release rather than their invasion from downstream reaches. Based on October sampling, it was likely all rainbow trout and cutthroat trout were removed but possible that some brown trout might remain. Nonetheless, hatchery-produced age-0 ( $\approx 100$  mm total length) Gila trout were released throughout upper Black Canyon in November 1998.

Black Canyon was next sampled in July 2001 and only native fishes were captured. Gila trout was most common in the upper-most reach (Aspen-Falls) and represented by several size classes, including age-0 individuals ( $<90$  mm TL). Speckled dace was the most common fish in both sampled reaches (Barrier-Private reach not sampled in 2001).

The absence of nonnative trout in Black Canyon in 2001 indicated the 1998 removal effort had been successful. In addition, the presence of Gila trout  $<90$  mm TL confirmed in-stream reproduction. At this point, it appeared that Black Canyon could support a mixed warmwater-coldwater assemblage, and the decision was made to not sample Black Canyon for several years. When next sampled in 2008, multiple size classes of brown trout were found throughout Black Canyon upstream of the fish movement barrier. These fish were either progeny of individuals that survived the 1998 mechanical removal effort or individuals and progeny of brown trout that traversed the gabion basket barrier, or both. In 2009, the gabion fish movement barrier was replaced with a concrete structure that presumably was more effective in precluding fish passage to upper reaches.

Beginning in 2008, the paramount management imperative was to suppress or eliminate brown trout so that a viable Gila trout population could be maintained in Black Canyon. A second objective was to document the dynamics of a mixed native warmwater-coldwater fish assemblage. Our expectation was that in time Gila trout would occur primarily, if not exclusively, in upstream, colder reaches (i.e., Aspen-Falls), that reproduction and recruitment by Gila trout would be limited, and that reference Gila trout populations would be demonstrably more robust (e.g., abundance, condition, and size structure) than the population in Black Canyon. Among native warmwater species, we anticipated that speckled dace and desert sucker would be the most successful (e.g., distribution, abundance, and size structure) and that longfin dace and Sonora sucker might maintain smaller populations in upper Black Canyon. The presence of brown trout would provide an opportunity to

characterize, if not quantify, the impact of a nonnative predator and competitor on native fishes.

In addition to the presence of a nonnative predator, global warming (Kennedy et al. 2008) was expected to present another challenge to maintenance of a viable Gila trout population in Black Canyon. Regional metrics indicate that the upper Gila River drainage climate is warming, that total annual precipitation is declining, and river flow regimes have been altered. While regional metrics do not reflect exactly the climatic and hydrologic conditions in Black Canyon over this period, they do indicate the changes that have likely occurred—increasing air temperatures, diminished summer flows, altered flow regimes, and elevated water temperatures.

Our purpose herein is to use information obtained on an assemblage of native warmwater fishes and Gila trout to determine if such communities have long-term viability. Specifically, we wished to determine if somatic and demographic attributes of Gila trout in such a mixed assemblage were demonstrably different from those attributes in solely Gila trout populations. In addition, we wished to characterize somatic and demographic attributes of the native warmwater species in the presence of Gila trout. And finally, to evaluate efficacy of mechanical removal of a nonnative salmonid.

### 3 Approach

*Study Area*—Black Canyon lies entirely within the Gila National Forest of southwestern New Mexico, USA and almost its entire course is within designated wilderness (Aldo Leopold and Gila Wildernesses). From its origins in the Black Range (elevation ca. 2450 m), Black Canyon flows east to join East Fork Gila River (elevation 1770 m) a short distance upstream of the latter's confluence with the Gila River (Fig. 2). The study area was in the upper 17 km of Black Canyon, extending from the fish movement barrier (elevation 2074 m) upstream to the confluence of Falls Canyon (elevation 2440 m). In upper reaches, the stream was canyon-bound and bordered by mixed conifers (white fir *Abies concolor* and Douglas fir *Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*). Near Aspen Canyon confluence, the stream entered a broad valley with scattered ponderosa pine stands and Gambel oak (*Quercus gambellii*) (Fig. 3). Downstream of Bonner Canyon, the stream progressed through more constricted terrain to the fish movement barrier. Riparian vegetation consisted of ponderosa pine, narrow leaf cottonwood (*Populus angustifolia*), and willow (*Salix* sp) was scattered among ponderosa pines along the stream. Three tributaries joined Black Canyon in its course within the study area; Falls Canyon was perennial, and Aspen and Bonner canyons were intermittent. Fish did not occur above the waterfalls a short distance (ca. 50 m) upstream of the confluence of Black and Falls canyons.

*Methods*—The study area was divided into four sampling reaches. The most upstream and canyon-bound reach extended from Aspen Canyon to Falls Canyon confluence (8.7 km). The middle valley reach was from the upstream boundary of a

**Fig. 3** Black Canyon near confluence of Aspen Canyon, New Mexico



small private inholding to Aspen Canyon (5.8 km). The penultimate downstream reach was from the fish movement barrier to the downstream boundary of the private property (1.3 km). The stream was not sampled in the 1.1 km private property reach. And the lowest was a 3-km reach downstream of the fish movement barrier. Nonnative salmonids were not removed from this reach, and it was accessible to fishes from downstream reaches and tributaries (Whitney et al. 2017; Hedden et al. 2022). Species codes (first three letters of genus and species, e.g., AGOCHR = *Agosia chrysogaster* longfin dace and ONCGIL = *Oncorhynchus gilae* Gila trout) were used on graphs and tables to conserve space.

Following release of Gila trout in 1998, Black Canyon was not sampled until 2001. After a 7-year hiatus, it was again sampled in 2008. Thence, the stream was sampled annually in July or August through 2012. The extent of the study area sampled in a year was dependent upon personnel availability and weather; the Barrier-Private reach was sampled in all years (June in 2008), Private-Aspen reach in all years, and Aspen-Falls reach in 2008, 2011, and 2012. The fish assemblage downstream of the barrier was sampled multiple times prior to, during, and after the 2008–2012 sampling period. The Below Barrier reach data are presented to provide a contrast to above barrier data. Two or three crews, each composed of 3–5 individuals and sampling in different stream sections, used battery-powered backpack

shockers to stun fish. Stunned fish were netted and mass ( $\pm 1$  g) and total length ( $\pm 1$  mm, TL) of large-bodied individuals ( $\geq 100$  mm TL) determined. Small-bodied individuals were typically only counted, but in several years, TL was measured for subsamples of small-bodied fishes. In 2011, small-bodied fishes were not counted; elevated water temperatures and handling stress necessitated rapid processing of fish to reduce mortality. All fish, except nonnative brown trout, were returned to stream near point of capture. Abundance was the number of individuals captured/elapsed time electrofishing (#/min).

Water temperature data were obtained from temperature loggers deployed by New Mexico Surface Water Quality Bureau (NM Environment Department). Regional precipitation and temperature data 1980 through 2020 were obtained from four weather stations in the upper Gila River drainage (USGS HUC # 15040001) NOAA website ([www.ncdc.noaa.gov/cdo-web](http://www.ncdc.noaa.gov/cdo-web)). Two stations (Lookout Mountain and Signal Peak) were at high elevations (2591 m and 2548 m, respectively) and the remaining two (Beaverhead and Gila Hot Springs) were somewhat lower (2033 m and 1718 m, respectively). Gila River discharge data were obtained from the USGS Gila River near Gila gage (# 09430500).

Three metrics were used to characterize the well-being of Gila trout, brown trout, Sonora sucker, and desert sucker: condition, size structure, and abundance (catch-per-unit-effort: #/min elapsed electrofishing time). Because Gila trout have near isometric growth (i.e.,  $W = aL^3$ ) throughout their lives, Fulton's Condition Factor was used to estimate general physiological condition of Gila and brown trout (Pope and Kruse 2007). The factor is determined by  $K_{TL} = (\text{Mass}/\text{Total Length}^3) * 10^5$ . Because condition was normally distributed for each year and reach, ANOVA was used to compare mean condition between years, reaches, and populations. The Kolmogorov–Smirnov Goodness of Fit two-sample test was used to compare annual intra-reach, inter-reach, and population size structure (Neumann and Allen 2007). Specimens were grouped in 10-mm TL classes for K-S analysis. Gila trout specimens  $< 70$  mm TL (age 0) and brown trout specimens  $< 100$  mm TL were excluded from analyses. All statistical procedures were done with XLSTAT (Addinsoft 2021).

Reference Gila trout populations were in McKnight and Diamond creeks. Diamond Creek (elevation ca. 2430 m) was about 14 air km north of Black Canyon while McKnight Creek (elevation ca. 2340 m) was about 14 air km south of Black Canyon. Both streams were roughly comparable to Black Canyon in habitat dimensions (stream width, depth, and discharge) but upper Black Canyon was substantially longer ( $\approx 18$  km) than Diamond Creek ( $\approx 6$  km) and McKnight Creek ( $\approx 8$  km). There was no stream unaffected by wildfire and drought within the current range of Gila trout that also had a mixed warmwater-coldwater assemblage that might serve as a reference for mixed assemblage or warmwater species comparisons. Black Canyon downstream of the fish movement barrier was sampled (nonnative salmonids not removed) relatively frequently from 1996 through 2021 and thus provided some perspective on the changes in the fish assemblage in upstream reaches.

Following an initial stocking of age-0 (70–115 mm TL, number not recorded) hatchery-produced Gila trout in Black Canyon upstream of the barrier in late 1998, it was stocked annually thereafter in autumn. Numbers released annually ranged

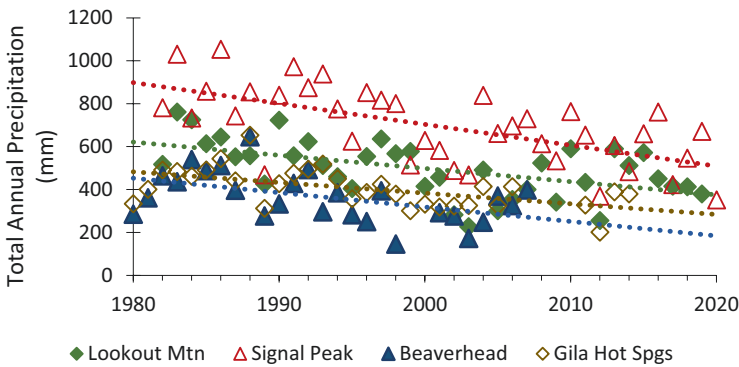


from several hundred to several thousand. Most releases were of age-0 fishes (80–115 mm TL), but two releases were of larger and older fish (105 individuals averaging about 300 mm TL in 2009 and about 1000 individuals averaging 150 mm TL in 2016). Individuals <100 mm TL were considered juveniles, those between 101 and 150 sub-adults, and >150 adults (Propst and Stefferud 1997).

### 4 Results

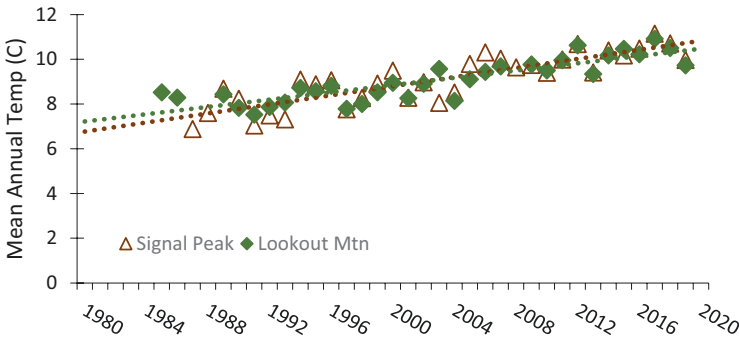
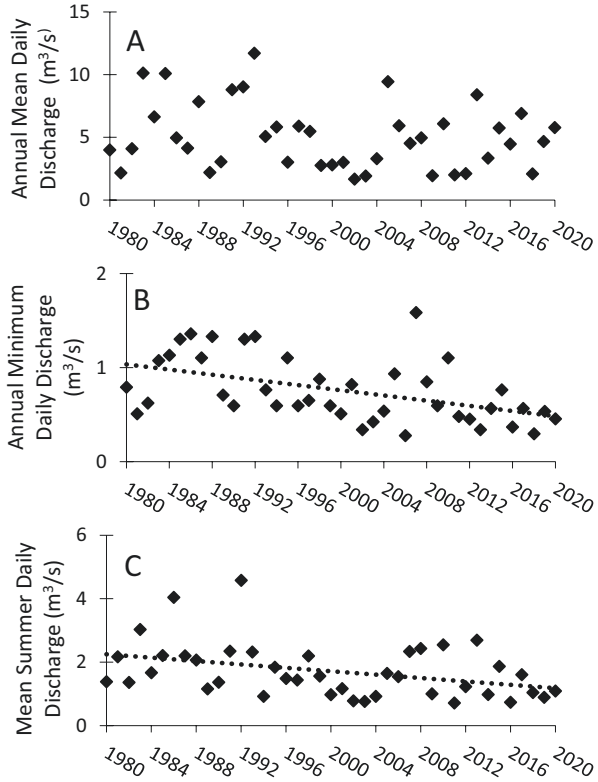
*Regional Climatic, Discharge, and Water Temperature Patterns (1980–2020)*—Total annual precipitation over the past 40 years has declined significantly at four upper Gila River catchment weather stations (Fig. 4). Although total annual precipitation declined, mean daily discharge at the Gila River near Gila gage did not (Fig. 5). However, extreme flow events (floods and minimum flows) increased. Since 1980, there have been 10 annual peak flows exceeding 283 m<sup>3</sup>/s (=10<sup>4</sup> ft<sup>3</sup>/s), whereas in the preceding 51 years there were only 4 years with peak flows greater than 283 m<sup>3</sup>/s. Annual minimum daily discharge and summer (June and July) mean daily discharge decreased over the 1980–2020 period. At the two weather stations that recorded mean daily air temperature, mean annual temperature increased significantly (Fig. 6). Temperature loggers deployed upstream of Aspen Canyon confluence and at Aldo Leopold Wilderness boundary recorded mean daily water temperatures in 2012 approaching 20 °C, but maximum daily water temperatures exceeded 25 °C frequently in June at both locations and less frequently in July and August (Fig. 7).

*Temporal Changes in Fish Assemblage*—Although the upper Black Canyon fish assemblage was greatly reduced, if not eliminated, by ash- and sediment-laden flows associated with the 1995 Bonner Fire, native cyprinids and catostomids were comparatively common in the Below Barrier reach a year after the fire and



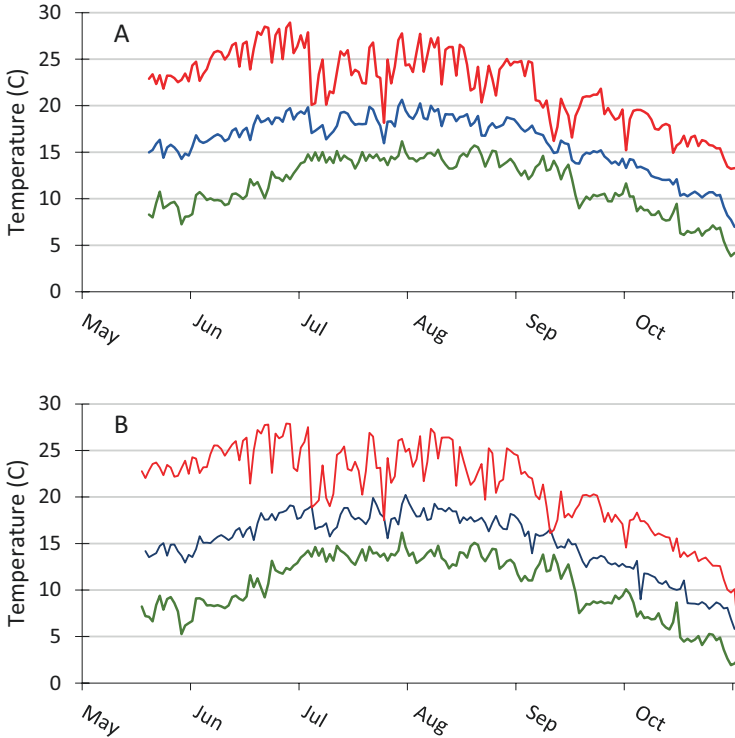
**Fig. 4** Total annual precipitation at four weather stations in the upper Gila River catchment. Dashed lines indicate significant ( $\alpha = 0.05$ ) relationship

**Fig. 5** Discharge attributes of Gila River at USGS Gila River near Gila gage (09430500), New Mexico. Dashed lines indicate significant ( $\alpha = 0.05$ ) relationship

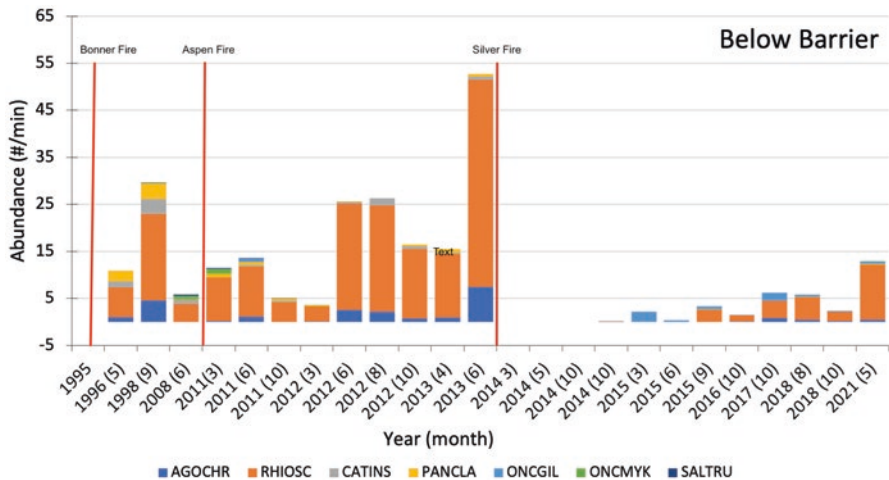


**Fig. 6** Mean annual air temperature at two weather stations in upper Gila River catchment, New Mexico. Dashed lines indicate significant ( $\alpha = 0.05$ ) relationship

especially in 1998 (Fig. 8). Speckled dace was the most common species in all collections and nonnative salmonids were rare. Although abundance was variable across collections, fish numbers, especially speckled dace, increased substantially in 2012 and 2013, crashed following ash and sediment flows caused by the 2013 Silver Fire, and no fish was collected in this reach until October 2014 when 12



**Fig. 7** Mean, maximum, and minimum daily water temperature in Black Canyon at Aldo Leopold Wilderness boundary (a) and just upstream of Aspen Canyon confluence (b), New Mexico, May–October 2012



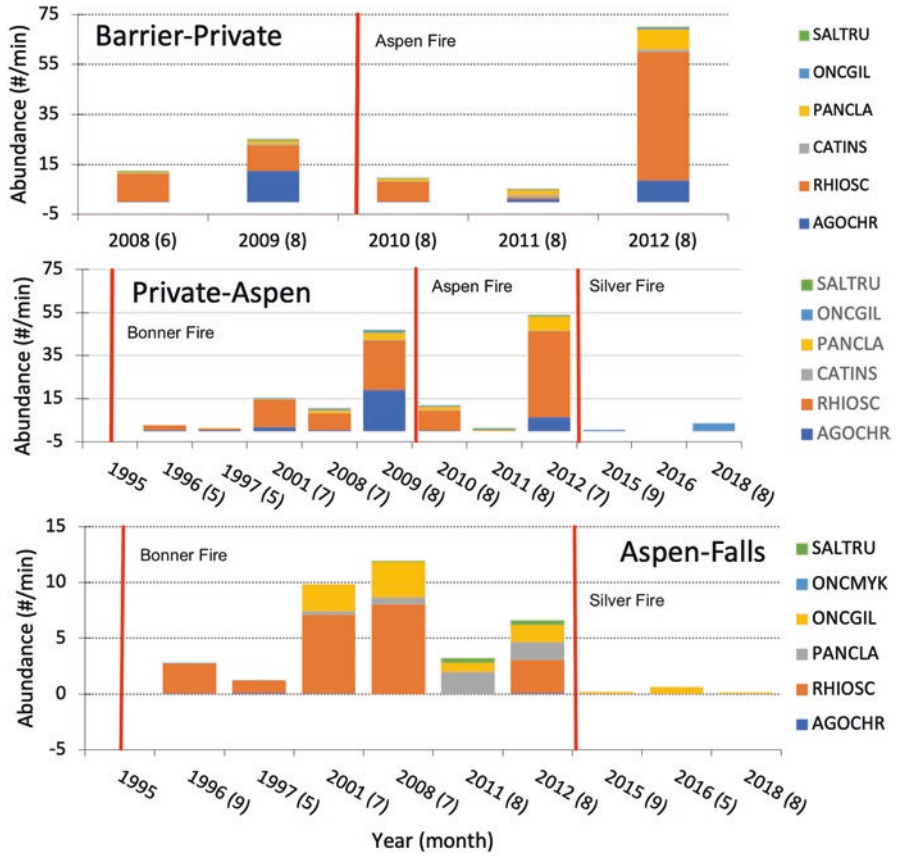
**Fig. 8** Abundance (#/min) of fishes in Black Canyon Below Barrier reach, New Mexico, 1996–2021. Month of sampling in parentheses

speckled dace and a single Gila trout were collected. Thereafter, fish abundance increased slightly through 2021 but remained considerably less than in the collections preceding the Silver Fire.

Within a year of the Bonner Fire, native fishes moved from downstream refugia to the upper reaches of Black Canyon. Thereafter, fish abundance in the reaches upstream of the barrier generally increased through 2012 (Fig. 9). Ash and sediment flows associated with the Aspen Fire contributed to the comparatively low abundance of fishes in the Barrier-Private and Private-Aspen reaches in 2010. Speckled dace was typically the most common fish in all reaches in all years; low abundance of fishes in 2011 was largely a reflection of partially counting small-bodied fishes in the Barrier-Private reach and not counting them in the Private-Aspen and Aspen-Falls reaches. Neither brown nor Gila trout was common in any reach in 2011 but desert sucker was moderately common in the Aspen-Falls reach. In 2012, fishes attained their greatest abundance in the Barrier-Private and Private-Aspen reaches while that in the Aspen-Falls reach was moderately high. The 2013 Silver Fire eliminated fishes from all reaches (Fig. 10). In 2013 and subsequent years, hatchery-reared Gila trout were released in autumn at several locations in the above-barrier reaches. Most, if not all, Gila trout captured in the Aspen-Falls reach in 2016 were hatchery-produced fish. But in August 2018, a large portion of the sample in the Private-Aspen reach was age-0 fish (<90 mm TL), which were almost certainly spawned in the stream. The fish movement barrier precluded the natural colonization of the upper reaches of Black Canyon by native warmwater species.

*Longitudinal Abundance of Fishes*—Although variable from year to year, abundance of warmwater species generally declined from down- to upstream (Fig. 11). In average, longfin dace and speckled dace were roughly equally abundant in the Barrier-Private and Private-Aspen reaches and rare or uncommon in the most upstream reach. Sonora sucker was most common in the Barrier-Private reach and absent in the most upstream. Desert sucker abundance was greatest in the Barrier-Private reach, and it was more common in the most upstream reach than other warmwater species. Gila trout abundance increased from lowest to most upstream reach. In contrast, brown trout abundance was greatest in the middle reaches, and there its abundance was low compared to Gila trout. Since the 2013 Silver Fire only Gila trout occupy the reaches upstream of the fish movement barrier.

*Size structure of Black Canyon Gila Trout Population and Reference Populations*—During 2008–2012, the number of Gila trout captured varied considerably across reaches and years within each reach (Table 1). Age-0 individuals ( $\leq 90$  mm TL) were rarely collected in any reach in any year (Fig. 12). An unknown portion of the fishes collected each year in each reach in July–August were hatchery-produced fish. When stocked (typically October or November) most releases were comprised of age-0 (<130 mm TL) but in 3 years larger fish (157–196 mm TL) were



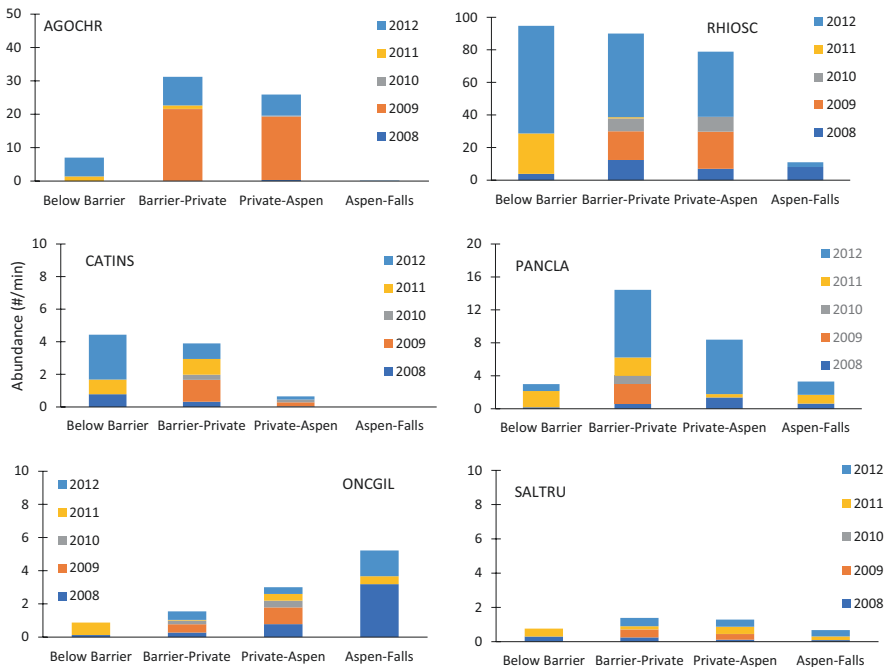
**Fig. 9** Abundance (#/min) of fishes in Black Canyon reaches upstream of fish movement barrier, 1996–2018. Aspen Fire not indicated on Aspen-Falls reach because it did not burn in Aspen-Falls catchment. Note different abundance axes

released and in 2009 about 100 >275 mm TL were released (Table 2). Some stocked fish likely survived to be collected the following year as age-1 individuals between 100- and 150-mm TL. And some stocked fish survived for multiple years. Most collections were comprised largely of fish <200 mm TL, but in several years fish >200 mm was a substantial portion of the collection (e.g., 2010 and 2011 in Private-Aspen reach).

Size structure of Gila trout in each reach across years was generally similar. Between year differences in size structure were different for only two comparisons:



**Fig. 10** Debris and fine sediment deposits in Black Canyon in Barrier-Private reach following the 2013 Silver Fire



**Fig. 11** Abundance of fishes from most downstream reach to most upstream. The Below Barrier and Aspen-Falls reaches were not sampled in 2009 and 2010. The Below Barrier reach was sampled one (2008), three (2011), and four (2012) times. In 2011, small-bodied fishes in Private-Aspen and Aspen-Falls reaches were not counted. Note different scales on Abundance axis

**Table 1** Black Canyon Gila trout population and reference population statistics, 2001 and 2008–2012

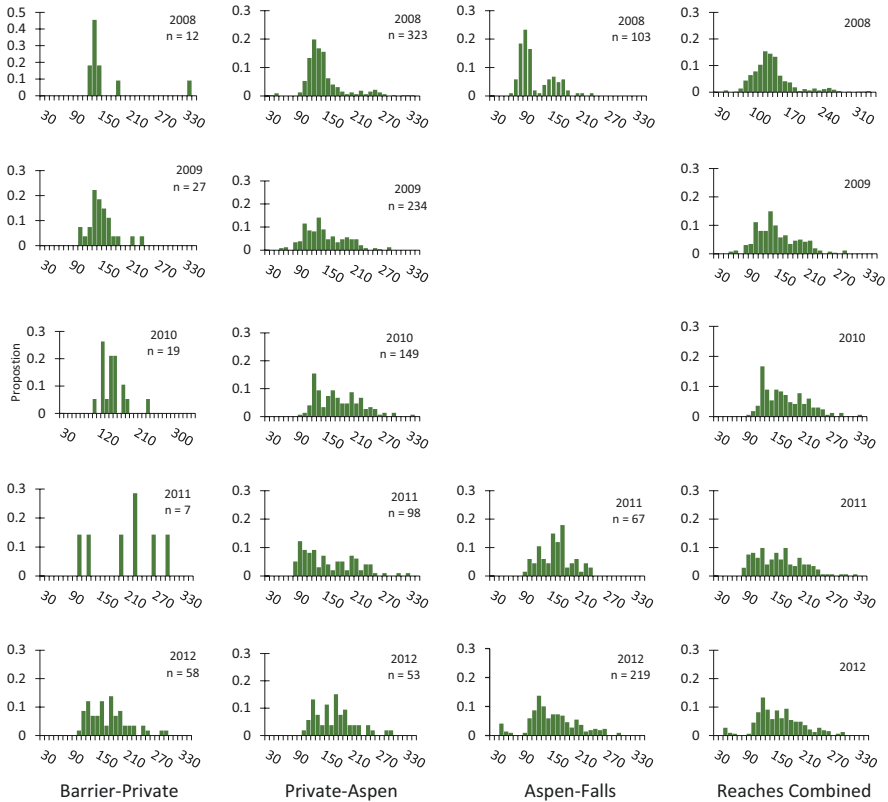
Population		Year	Month	N (TL)	TL range (mm)	TL mean (mm)	N (mass)	Mass mean (g)
Black	Barrier-Private	2008	Jun	12	126–340	159.0	11	55.8
		2009	Aug	27	110–233	149.3	27	29.5
		2010	Aug	19	105–233	151.1	19	39.1
		2011	Aug	7	101–300	205.9	7	126.0
		2012	Aug	58	106–300	169.5	57	54.9
	Private-Aspen	2001	Jul	13	40–223	90.5	8	31.0
		2008	Jun	82	105–215	134.6	65	26.2
		2008	Jul	257	40–335	149.9	248	46.1
		2009	Aug	246	55–290	149.0	234	41.3
		2010	Aug	149	95–340	176.8	148	70.5
		2011	Aug	98	81–327	157.7	97	49.0
	Aspen-Falls	2012	Jul	53	106–300	172.8	51	59.1
		2001	Jul	100	24–270	76.46	33	52.1
		2008	Jul	103	70–231	116.5	100	20.8
		2011	Aug	67	99–239	162.1	67	43.6
Diamond		2012	Aug	219	41–300	154.3	204	49.3
		2001	Jul	138	70–203	115.8	138	18.8
		2008	Apr	83	42–241	129.4	65	37.4
McKnight		2010	Oct	386	47–240	117.8	294	24.6
		2011	Jul	235	64–185	122.8	235	21.1

Barrier-Private 2011–2012 and Aspen-Falls 2011–2012 samples (Table 3). Size structure was different for all Barrier-Private/Private-Aspen comparisons, except 2012 (Table 4). The size structure of the 2012 Private-Aspen/Aspen-Falls samples was different.

The size structure of the Black Canyon Gila trout population was different from that of the Diamond population in 2008 and McKnight population in 2011 (Table 5). Figure 13 illustrates the differences in size structure of the populations. In both Diamond and McKnight creeks maximum specimen TL rarely exceeded 220 mm whereas in Black Canyon several individuals in most years exceeded >300 mm TL.

Post-Silver Fire monitoring of the above barrier Gila trout population was initiated in 2015. Most, if not all fish, collected in 2015 and 2016 were hatchery-produced individuals (Fig. 14). In 2018, however, a substantial number of age-0 (<90 mm TL) individuals were collected.

*Condition ( $K_{TL}$ ) of Black Canyon Gila Trout and Reference Populations*—Mean Gila trout condition was >0.9000 in all years in all Black Canyon reaches, except Barrier-Private in 2009 when it was 0.8341 (Table 6). Most variation in mean annual



**Fig. 12** Size structure of Black Canyon Gila trout population, 2008–2012

condition was in the Barrier-Private reach. Mean condition of Gila trout in the Barrier-Private reach in 2009 was significantly less than that in 2008 and 2010 (Table 7). In 2011, mean condition in the reach was greater than that in 2012 but not 2010. In the Private-Aspen reach, annual mean condition differences from 2008–2009 through 2010–2011 were significant but that of 2011–2012 was not. Only two Barrier-Private/Private-Aspen condition comparisons were different; condition was less in Barrier-Private reach in 2009, but greater in 2011 (Table 8). All Private-Aspen/Aspen-Falls comparisons were non-significant; mean condition of the 2011 Private-Aspen/Aspen-Falls samples was virtually identical. In two of four population condition comparisons,  $K_{TL}$  of the Black Canyon population was greater than that of the reference population and less in the other two (Table 9). All population comparisons yielded significant differences.

*Brown Trout Population Attributes*—Although absent in 2001, brown trout occurred throughout the upper reaches of Black Canyon in 2008. Despite annual efforts (2008–2012) to suppress their numbers by removing all individuals captured, the number captured generally increased over time (Table 10). The size



**Table 2** Hatchery-reared GT stocked in Black Canyon, New Mexico. Numbers released in 1998 and 1999 not recorded

Year	Date	Number	Mean TL (mm) <sup>a</sup>
1998	Nov		
1999	20 Oct		
2000	1 Nov	1872	80
2001	31 Oct	2000	
2002	–	2000	–
2004	–	2160	190
2005	–	445	91
2006	–	2815	81
2007	–	288	196
2009	22 Dec	900	107
2009	22 Dec	105	297
2011	21 Nov	1045	130
2012	31 Oct	1022	102
2013	23 Oct	1007	114
2013	4 Dec	2169	119
2014	23 Oct	3167	109
2015	22 Sep	3514	89
2016	29 Mar	1015	157
2017	25 Sep	4112	104

<sup>a</sup>Converted from English units

**Table 3** Black Canyon intra-reach Kolmogorov–Smirnov Goodness of Fit Test results comparing Gila trout size structure (10-mm size classes) year-to-year in each reach (specimens <70 mm TL excluded). Shaded cells indicate significant ( $\alpha = 0.05$ ) differences in size structure

Reach	Years	Months	D	p
Barrier-Private	2008-2009	Jun-Aug	0.207	0.149
	2009-2010	Aug-Aug	0.103	0.780
	2010-2011	Aug-Aug	0.103	0.588
	2011-2012	Aug-Aug	0.414	0.001
Private-Aspen	2008-2009	Jul-Aug	0.172	0.662
	2009-2010	Aug-Aug	0.207	0.459
	2010-2011	Aug-Aug	0.207	0.414
	2011-2012	Aug-Jul	0.241	0.186
Aspen-Falls	2011-2012	Aug-Aug	0.345	0.041

**Table 4** Black Canyon inter-reach Kolmogorov–Smirnov Goodness of Fit Test results comparing annual Gila trout size structure (10-mm size classes) between reaches (specimens <70 mm TL excluded). Shaded cells indicate significant ( $\alpha = 0.05$ ) difference in size structure

Year	Barrier-Private/Private-Aspen		Private-Aspen/Aspen-Falls	
	D	p	D	p
2008	0.621	<0.0001	0.276	0.132
2009	0.483	0.001		
2010	0.483	0.001		
2011	0.552	<0.0001	0.207	0.396
2012	0.069	0.996	0.345	0.042

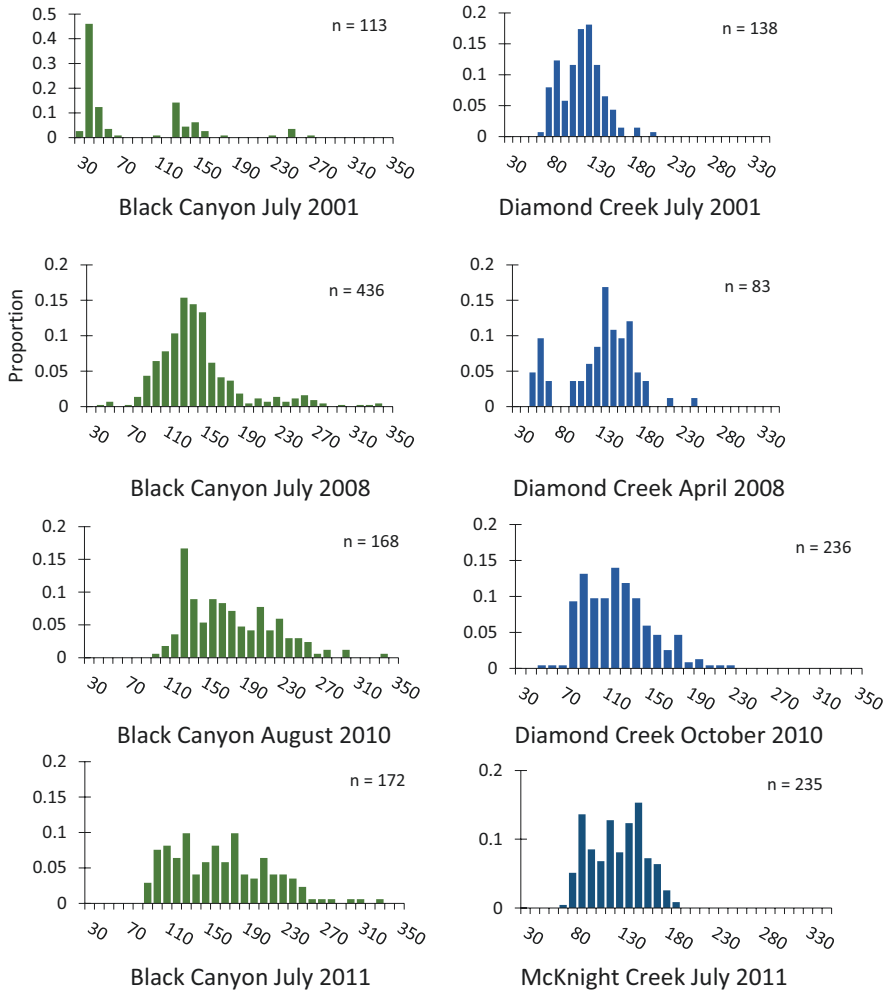
**Table 5** Kolmogorov–Smirnov Goodness of Fit Test results for Black Canyon population and reference populations size-structure comparisons (10-mm TL size classes). Shaded cells indicate significant ( $\alpha = 0.05$ ) differences in size structure

Populations	Months	Blk TL	Blk TL range	Ref TL	Ref TL range	D	p
Black-Diamond 2001	Jul-Jul	125	70-227	116	70-203	0.241	0.118
Black-Diamond 2008	Jul-Apr	141	70-340	146	91-241	0.483	0.001
Black-Diamond 2010	Aug-Oct	174	95-340	119	71-226	0.207	0.408
Black-McKnight 2011	Jul-Jul	161	81-327	123	72-185	0.379	0.021

structure of the population (reaches combined) indicated that reproduction and recruitment occurred each year from 2007 through 2011, except 2008 (Fig. 15). Most individuals collected were <300 mm TL, but larger individuals were found each year. No between year size-structure differences were detected (Table 11). Mean condition of brown trout each year >1.0000 in all years (Table 12). Between year condition was different in 2009–2010 and 2010–2011 (Table 13).

*Mass of Gila and Brown Trout*—Total mass of collected Gila trout (excluding individuals <70 mm TL) was variable across years and reaches (Table 14). It generally increased in Barrier-Private and Aspen-Falls reaches from 2008 through 2012. In Private-Aspen reach, total mass was greatest in 2008 and steadily declined to its lowest in 2012. In years all reaches were sampled, total Gila trout mass was least in 2011 and greatest in 2012. Brown trout total mass (excluding individuals <70 mm TL) was likewise variable among reaches and year to year. It was greatest in Barrier-Private and Aspen-Falls in 2012. Total brown trout mass increased from 2008 through 2012. Brown trout mass exceeded that of Gila trout in all years in Barrier-Private, all but one in Private-Aspen, and never in Aspen-Falls.

*Warmwater Species Population Attributes*—Because large numbers of desert sucker were often collected, TL and mass were obtained from a representative subsample of desert suckers collected in each reach each year. For example, in the Private-Aspen reach in 2008, 595 desert suckers were captured, TL was obtained from 131 and mass determined for 126. Desert sucker abundance generally increased from 2008 through 2012 (Table 15). Although the range of TL was similar across years, mean TL was more variable (Fig. 16). Size structure of the Black Canyon desert sucker population, however, did not differ from one year to the next (Table 16). Mean annual condition of desert suckers exceeded 1.1 in all years and was greatest

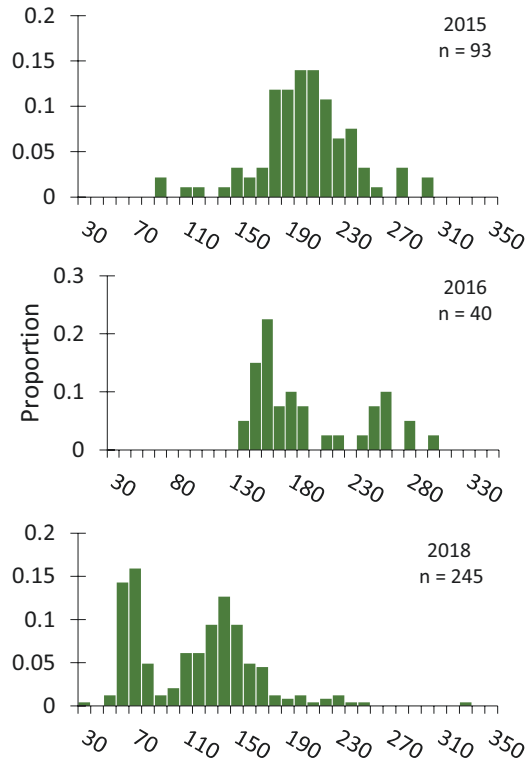


**Fig. 13** Size structure of Black Canyon Gila trout population and that of its reference populations. 2008 Black Canyon—Diamond Creek and 2011 Black Canyon—McKnight Creek were significantly different (see Table 5). Note different proportion axis scale on Black Canyon July 2001 graph

in 2010 (Table 17). Between year mean condition differences were different for all years (Table 18).

The TL range of Sonora suckers captured each year indicated multiple age classes and annual reproduction (Table 19). Most individuals were between 100- and 250-mm TL but several larger fish were captured in all years (Fig. 17). Size structure of the population did not differ from year to year (Table 20). Mean condition of the population exceeded 1.2 in all years but 2009 when it was slightly less (Table 21). Mean condition was different only between 2009 and 2010 (Table 22).

**Fig. 14** Post-Silver Fire size structure of Gila trout population in Black Canyon upstream of fish movement barrier. The September 2015 and August 2018 samples were taken in Private-Aspen and Aspen-Falls reaches whereas the May 2016 sample was from the Aspen-Falls reach. Note the different proportion axis scale for the 2016 collection



**Table 6** Fulton’s Condition Index ( $K_{TL}$ ) of Gila trout in Black Canyon. Individuals <70 mm excluded

Reach	Year	Month	n	$K_{TL}$ range	$K_{TL}$ mean
Barrier-Private	2008	Jun	11	0.8396–1.0734	0.9638
	2009	Aug	27	0.5788–1.1285	0.8341
	2010	Aug	19	0.9060–1.2649	0.9878
	2011	Aug	7	0.8392–1.7326	1.0672
	2012	Aug	56	0.6818–0.9149	0.9149
Private-Aspen	2008	Jul	245	0.6575–1.3994	1.0206
	2009	Aug	232	0.6164–1.5313	0.9621
	2010	Aug	110	0.8017–1.3432	0.9937
	2011	Aug	87	0.6420–1.2298	0.9133
	2012	Aug	51	0.6818–1.2301	0.9206
Aspen-Falls	2008	Jul	97	0.7073–1.2644	0.9735
	2011	Aug	67	0.6717–1.2288	0.9366
	2012	Aug	204	0.6575–1.2660	0.9377

**Table 7** Black Canyon intra-reach condition annual comparisons ANOVA results. Shaded cells indicate significant differences in mean  $K_{TL}$ .

Reach	Years	Months	F	p	d.f
Barrier-Private	2008-2009	Jun-Aug	7.796	0.008	1,36
	2009-2010	Aug-Aug	17.133	<0.0001	1,44
	2010-2011	Aug-Aug	1.114	0.302	1,24
	2011-2012	Aug-Aug	5.479	0.022	1,62
Private-Aspen	2008-2009	Jul-Aug	13.326	<0.0001	1,545
	2009-2010	Aug-Aug	3.930	0.048	1,342
	2010-2011	Aug-Aug	32.376	<0.0001	1,195
	2011-2012	Aug-Jul	0.036	0.849	1,134
Aspen-Falls	2011-2012	Aug-Aug	0.084	0.772	1,136

**Table 8** Black Canyon annual inter-reach condition comparison ANOVA results. Shaded cells indicate significant differences in mean  $K_{TL}$ .

Year	Barrier-Private/Private-Aspen			Private-Aspen/Aspen-Falls		
	F	p	d.f.	F	p	d.f.
2008	0.764	0.383	1,321	2.644	0.105	1,411
2009	14.769	<0.0001	1,259			
2010	0.067	0.796	1,127			
2011	9.946	0.002	1,92	0.000	1.000	1,172
2012	0.218	0.641	1,104	0.161	0.689	1,98

**Table 9** Black Canyon Gila trout and reference populations condition ( $K_{TL}$ ) comparisons ANOVA results. Shaded cells indicate significant differences in mean  $K_{TL}$ .

Populations	Year	Months	Mean BLK $K_{TL}$	Mean REF $K_{TL}$	F	p	d.f.
Black-Diamond	2001	Jul-Jul	1.2224	1.0540	77.321	<0.0001	1,178
Black-Diamond	2008	Jun-Apr	1.0034	1.1010	25.023	<0.0001	1,487
Black-Diamond	2010	Aug-Oct	0.9934	0.9534	11.499	0.001	1,270
Black-McKnight	2011	Aug-Jul	0.9247	0.9822	27.123	<0.001	1,390

In 2008 and 2011, small subsamples of speckled dace were measured, and a larger subsample was measured in 2012 (Fig. 18a). Several individuals >100 mm TL were captured in 2008 and 2012. The size range of individuals collected indicated successful reproduction and recruitment each year. The abundance of speckled dace varied considerably from year to year but was greatest in 2012 (Fig. 18b).

A subsample of longfin dace in the 2011 and 2012 collections was measured. Most specimens were <65 mm TL (Fig. 18c). The presence of longfin dace <40 mm TL indicated successful reproduction in both years. Like speckled dace, longfin dace abundance varied considerably from year to year.

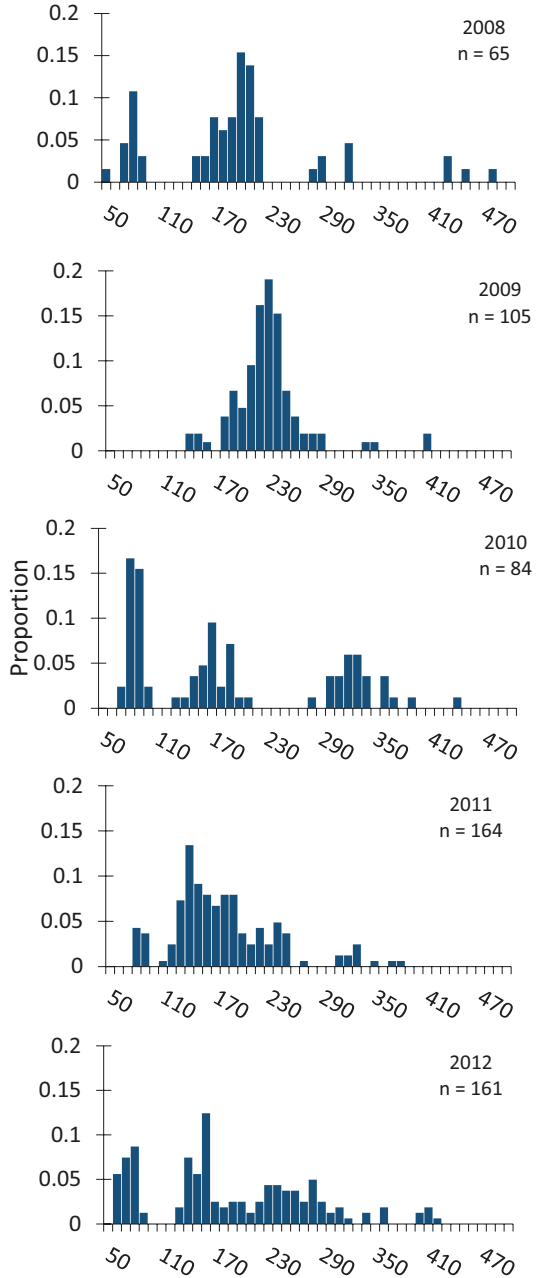
**Table 10** Black Canyon brown trout population statistics, 2008–2012

Reach	Year	Month	n	TL range (mm)	TL mean (mm)	Mass mean (g)
Barrier-Private	2008	Jun	11	154–472	271	343.2
	2009	Aug	25	152–247	213	97.7
	2010	Aug	11	70–360	134	87.8
	2011	Aug	32	126–371	178	74.1
	2012	Aug	55	55–403	189	128.6
Private-Aspen	2008	Jun	8	74–316	137	69.9
	2008	Jul	43	50–426	184	115.6
	2009	Aug	80	134–410	228	128.2
	2010	Aug	73	70–431	193	171
	2011	Aug	102	72–365	168	63.1
	2012	Jul	54	55–403	191	130.4
Aspen-Falls	2008	Jul	3	143–165	153	36.0
	2011	Aug	30	85–346	189	94.9
	2012	Aug	52	60–416	170	76.8

## 5 Implications and Conclusions

For species restricted to high elevation cool-coldwater habitats, climate change presents multiple challenges to their persistence. For Gila trout that naturally had a comparatively limited distribution in headwater reaches of streams draining the Mogollon Rim of central Arizona and southwest New Mexico (Behnke 2002), the contraction (within stream shrinkage of habitat) and reduction (loss of perennial streams) of suitable habitat imposes an additional layer of difficulty to its survival. Over past 20 years or so, climate models have predicted altered flow regimes and more extreme flow events (Stewart et al. 2005; Hamlet and Lettenmaier 2007; Wenger et al. 2011), increasing aridity (Seager et al. 2007; Seager and Vecchi 2010; Udall and Overpeck 2017; Overpeck and Udall 2020), elevated stream thermal regimes (Schultz et al. 2017), and more large and intense wildfires (Chikamoto et al. 2017; Brown et al. 2021). Exacerbating the changes wrought by extended drought (Cook et al. 2015; Ault 2020) is the increasing frequency and intensity of wildfire (Dennison et al. 2014; Abatzoglou and Williams 2016; Singleton et al. 2019). These projections and events are playing out over the upper Gila River catchment as illustrated by regional temperature, precipitation, stream flow records, and multiple large wildfires. Since 2000, 21 wildfires have each burned over 4050 ha on the Gila National Forest, including the 56,175 ha Silver Fire (Gila National Forest 2021). Over the past 40 years, total annual precipitation has decreased and mean annual ambient temperature has increased in the Gila River catchment. Both contribute to warming of streams that historically provided habitat for Gila trout. For a sibling species, Apache trout *Oncorhynchus apache*, median temperature for optimal growth must be below 19 °C and lower if daily fluctuations are >12 °C (Recsetar et al. 2014). Median 2012 summer (June–July) water temperatures in Black Canyon were 17.2 and 16.8 °C at Aldo Leopold Wilderness boundary and above Aspen

**Fig. 15** Size structure of the Black Canyon brown trout population upstream of fish movement barrier (reaches combined), 2008–2012. Aspen-Falls reach not sampled in 2009 and 2010



**Table 11** Black Canyon Kolmogorov–Smirnov Goodness of Fit Test results comparing brown trout inter-annual size structure (10 mm TL size classes). Reaches combined.

Years	Months	D	<i>p</i>
2008–2009	Jun–Aug	0.109	0.650
2009–2010	Aug–Aug	0.174	0.250
2010–2011	Aug–Aug	0.130	0.565
2011–2012	Aug–Jul	0.217	0.141

**Table 12** Fulton’s Condition Index ( $K_{TL}$ ) of brown trout in Black Canyon (reaches combined)

Year	Month	n	$K_{TL}$ range	$K_{TL}$ mean
2008	Jun	54	0.7148–1.8264	1.0535
2009	Aug	99	0.6886–1.4486	1.0339
2010	Aug	73	0.7527–1.7493	1.0842
2011	Aug	160	0.7111–2.1048	1.0239
2012	Aug	148	0.7148–1.8264	1.0294

**Table 13** Brown trout annual mean condition comparison ANOVA (reaches combined) results. Shaded cells indicate significant ( $\alpha = 0.05$ ) differences in mean condition

Years	Months	F	<i>p</i>	d.f.
2008-2009	Jun-Aug	0.462	0.498	1,151
2009-2010	Aug-Aug	4.760	0.030	1,170
2010-2011	Aug-Aug	7.864	0.005	1,231
2011-2012	Aug-Aug	0.143	0.706	1,310

**Table 14** Mass of Gila and brown trouts in upper Black Canyon (reaches combined), 2008–2012

Reach	Year	n	ONCGIL	n	SALTRU
			Total mass (kg)		Total mass (kg)
Barrier-Private	2008	11	0.640	10	3.532
	2009	27	0.797	25	2.442
	2010	19	0.743	11	0.996
	2011	7	0.882	32	2.371
	2012	57	3.131	54	6.945
Private-Aspen	2008	313	13.129	51	5.529
	2009	234	9.667	76	9.743
	2010	148	7.753	62	10.603
	2011	97	4.755	102	6.435
	2012	51	3.015	53	6.910
Aspen-Falls	2008	100	2.083	3	0.108
	2011	67	2.921	30	2.848
	2012	204	10.050	51	3.917



**Table 15** Black Canyon desert sucker population statistics (reaches combined), 2008–2012

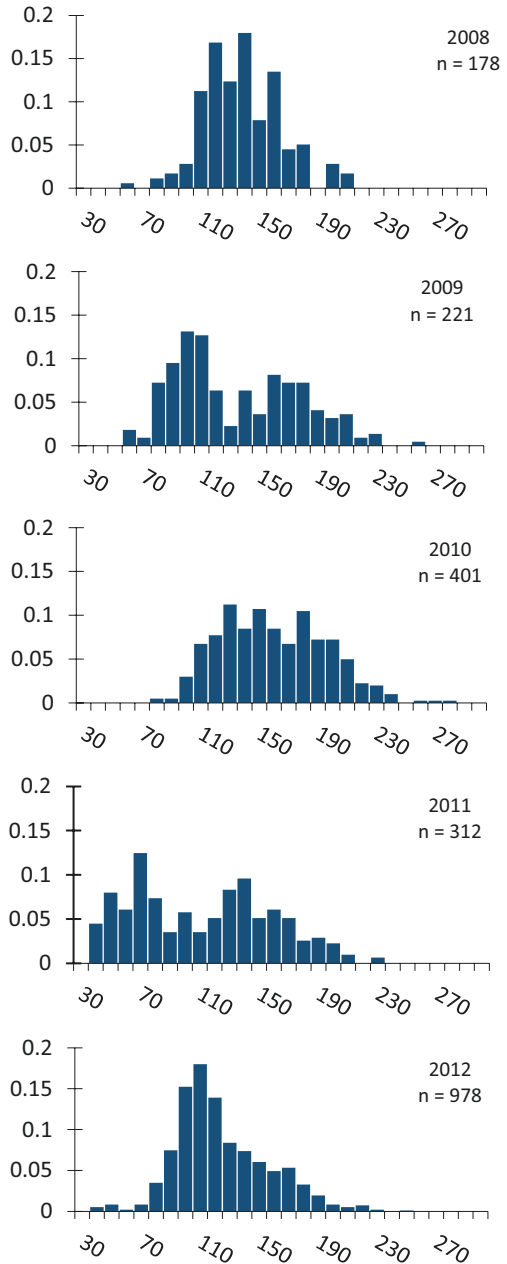
Year	Month	TL n	TL range (mm)	TL mean (mm)	Mass n	Mass mean (g)
2008	Jun	178	53–210	134.6	164	135.0
2009	Aug	221	53–259	130.0	219	190.0
2010	Aug	401	71–271	154.9	387	57.5
2011	Aug	312	32–225	107.1	134	32.2
2012	Jul & Aug	978	38–245	119.6	839	25.8

Canyon confluence, respectively, but daily fluctuations at both locations were  $>12^{\circ}$  almost every day in June 2012. Mean annual daily discharge in the Gila River has not declined since 1980, but frequency of days with extremely low mean discharge has increased substantially. Collectively, these metrics (wildfire frequency, declining annual precipitation, increasing ambient temperature, and altered flow regimes) indicate that many, if not all, streams within the upper Gila River catchment are becoming less suitable for maintaining Gila trout populations.

The elimination of fishes from upper Black Canyon by the 1995 Bonner Fire provided an opportunity to determine the potential for Gila trout to persist in a thermally compromised stream. And the movement of native warmwater species into upper Black Canyon added another dimension to evaluate: the potential for coexistence in a mixed warmwater-coldwater fish assemblage. An additional challenge for Gila trout and fellow native fishes was the return of nonnative piscivorous brown trout, especially individuals  $>175$  mm TL (Jonsson et al. 1999; Budy and Gaeta 2018), to upper Black Canyon.

The rapidity with which the four native warmwater species recolonized upper Black Canyon was impressive. Although the specific location of the refugia they survived ash and sediment flows in is uncertain, it is likely colonizers moved from perennial tributaries (Squaw and Apache creeks) about 12 river km downstream of the fish movement barrier and not affected by recent wildfires. Small-scale movement ( $\approx 2$  km) of Sonora sucker and desert sucker was documented by Booth and Shipley (2012) and Booth et al. (2013). Based on otolith microchemistry, Whitney et al. (2017) provided information indicating that speckled dace colonizers were likely from downstream Black Canyon tributaries or survived in the most downstream reaches of Black Canyon near the East Fork Gila River confluence. Although Whitney et al. (2017) did not have data to support longfin dace, Sonora sucker, or desert sucker movement from downstream tributaries, it is likely these refugia were the source of upstream colonizers. Presence of each native warmwater species in Squaw and Apache creeks and lower Black Canyon was confirmed in 2020 (Paggen, unpubl. data). If Squaw and Apache creeks were the source of colonizers, speckled dace moved over 20 km to the mid-reach of upper Black Canyon (about confluence of Aspen Canyon) in a year or less (July 1995–May 1996). The other species were all present in upper Black Canyon by 2001. By 2008, each species had substantial populations composed of multiple size classes in the lower two study reaches (Barrier-Private and Private-Aspen) and desert sucker regularly occurred in the upper-most reach (Aspen-Falls). Both speckled dace and desert sucker met our

**Fig. 16** Black Canyon desert sucker population size structure (reaches combined), 2008–2012



expectations that each would establish populations in the study reach but we did not expect that both longfin dace and Sonora sucker would also have multiple size-class populations in upper Black Canyon. Abundance of longfin dace was quite variable from year-to-year, indicating its status in upper Black Canyon was more tenuous than that of other native warmwater species.

**Table 16** Black Canyon desert sucker population inter-annual size structure Kolmogorov–Smirnov Goodness of Fit Test results

Years	Months	D	p
2008–2009	Jun–Aug	0.179	0.650
2009–2010	Aug–Aug	0.107	0.990
2010–2011	Aug–Aug	0.179	0.698
2011–2012	Aug–Aug	0.214	0.472

**Table 17** Black Canyon desert sucker annual condition (reaches combined), 2008–2012

Year	n	K <sub>TL</sub> range	K <sub>TL</sub> mean
2008	164	0.6982–2.4231	1.3299
2009	219	0.7124–3.3175	1.2459
2010	387	0.7154–2.5185	1.3073
2011	134	0.6361–1.9073	1.2162
2012	310	0.4158–1.5259	1.1482

**Table 18** Black Canyon desert sucker inter-year condition ANOVA results. Shaded cells indicate significance

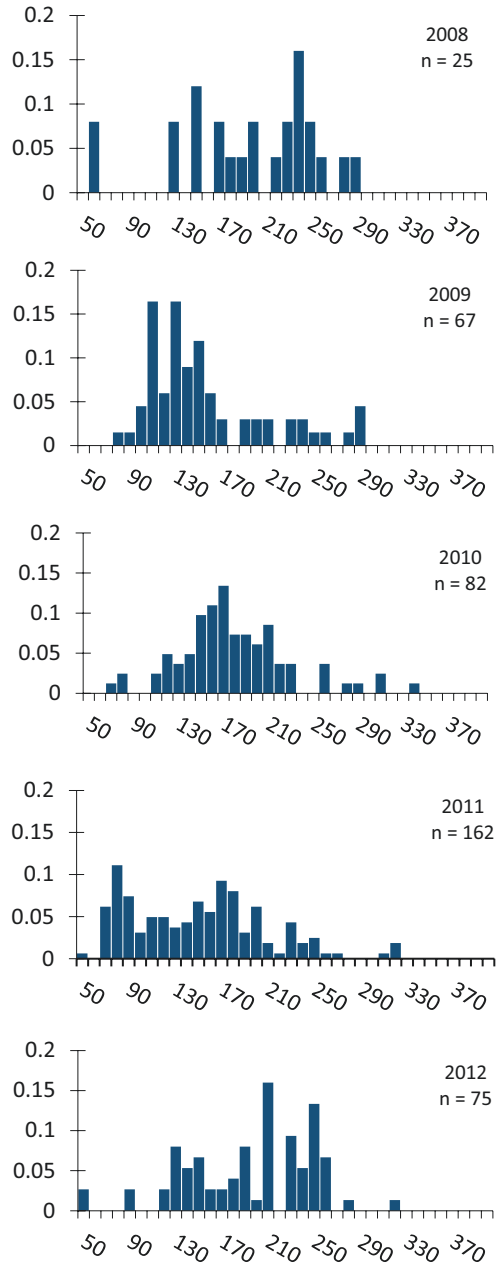
Years	Months	F	p	d.f.
2008-2009	Jun-Aug	11.519	0.001	1,381
2009-2010	Aug-Aug	14.513	0.000	1,604
2010-2011	Aug-Aug	29.383	<0.0001	1,519
2011-2012	Aug-Aug	17.404	<0.0001	1,442

**Table 19** Black Canyon Sonora sucker population statistics, 2008–2012 (reaches combined)

Year	Month	TL n	TL range (mm)	TL mean (mm)	Mass n	Mass mean (g)
2008	Jun	25	51–285	191.0	23	117.4
2009	Aug	67	72–290	151.2	67	58.9
2010	Aug	82	62–334	175.5	79	90.4
2011	Aug	162	40–319	145.6	124	71.2
2012	Aug	75	28–317	190.2	73	106.6

Gila trout lacked a pathway for a natural return to Black Canyon. The nearest Gila trout population, Diamond, was over 70 river km distant and where streams were perennial provided habitat for only warmwater species, including piscivorous smallmouth bass *Micropterus dolomieu* (Johnson et al. 2008). Thus, the annual release of hatchery-produced Gila trout in upper Black Canyon from 1998 through 2012 was necessary to establish and potentially maintain a population. Population augmentation, however, made determination of whether Black Canyon could sustain a naturally recruiting Gila trout population problematic. Using the presence of individuals <100 mm TL in August (i.e., Fig. 12) as an indicator of successful in-stream reproduction, there was limited survival of age-0 individuals in 3 years between 2008 and 2012. Nonetheless, from 2008 through 2012, multiple size classes were present in each above-barrier reach. When compared to reference populations, the size structure of Black Canyon was different in two comparisons

**Fig. 17** Black Canyon Sonora sucker population size structure (reaches combined), 2008–2012



**Table 20** Black Canyon Sonora sucker population inter-annual size-structure Kolmogorov-Smirnov Goodness of Fit Test results (reaches combined and individuals <100 mm TL excluded)

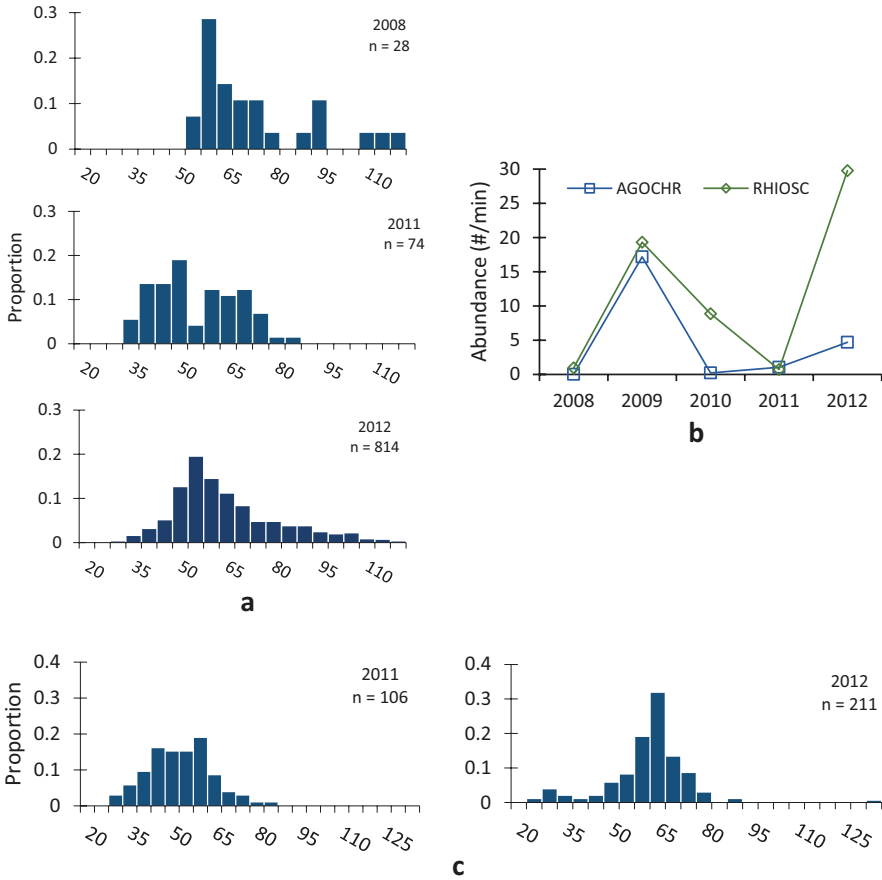
Years	Months	D	p
2008–2009	Jun–Aug	0.161	0.544
2009–2010	Aug–Aug	0.161	0.652
2010–2011	Aug–Aug	0.129	0.876
2011–2012	Aug–Aug	0.129	0.871

**Table 21** Black Canyon Sonora sucker population mean annual condition (reaches combined), 2008–2012

Year	n	K <sub>TL</sub> range	K <sub>TL</sub> mean
2008	23	1.0601–1.5411	1.2530
2009	67	0.7063–1.6789	1.1834
2010	79	1.0982–1.7403	1.2606
2011	124	0.7337–1.9877	1.2419
2012	73	0.7404–1.8441	1.2123

(Black-Diamond 2008 and Black-McKnight 2011), which was likely due to the number of large Gila trout (>250 mm TL) in Black Canyon and absence of any fish >250 mm TL in Diamond or McKnight creeks. Abundance of Gila trout in each Black Canyon reach was <1.0/min and varied considerably across years, especially in the Barrier-Private reach. Mean annual condition (K<sub>TL</sub>) exceeded 1.0 only once in each Barrier-Private and Private-Aspen. Comparisons of the Black Canyon population to reference populations did not yield consistent differences. For example, mean K<sub>TL</sub> of Black Canyon fishes was greater than reference population in two comparisons, but in two others the reference population K<sub>TL</sub> was greater. In 2012, the longitudinal distribution of Gila trout indicated that if Black Canyon was to support a viable Gila trout population it would be centered in the most upstream reaches.

The long-term potential for native warmwater species and Gila trout coexistence appeared possible based on the longitudinal distribution of native fishes in upper Black Canyon and the robust warmwater species populations. But could the Gila trout population persist without frequent augmentation and the continued suppression of nonnative piscivorous brown trout? The low numbers and irregular collection of age-0 Gila trout might reflect brown trout predation and the need for continued Gila trout augmentation. Brown trout tended to be more common in Barrier-Private and Private-Aspen reaches and Gila trout was more common in the Aspen-Falls reach. Whether this pattern was a consequence of brown trout occurring where there was abundant warmwater fish prey or other factor(s) is impossible to discern. Regardless of the specific reason(s) for the observed distribution pattern of brown trout, it was apparent that suppression efforts had to continue and likely be more frequent and intensive, similar to successful suppression efforts elsewhere (Healy et al. 2020), to enable a mixed warm-coldwater assemblage to coexist in Black Canyon.



**Fig. 18** (a) Black Canyon speckled dace population size structure (reaches combined), 2008, 2011, and 2012. (b) Abundance of speckled dace and longfin dace in Black Canyon, 2008–2012. A subsample of specimens of each species was tallied only in Barrier-Private reach in 2011. (c) Black Canyon longfin dace population size structure in Black Canyon (reaches combined), 2011 and 2012

**Table 22** Black Canyon Sonora sucker population inter-year condition comparison ANOVA results (reaches combined). Shaded cells indicate significant difference ( $\alpha = 0.05$ )

Years	Months	F	p	d.f.
2008-2009	Jun-Aug	0.274	0.602	1,90
2009-2010	Aug-Aug	9.234	0.003	1,144
2010-2011	Aug-Aug	0.635	0.426	1,201
2011-2012	Aug-Aug	1.069	0.302	1,195

Our study ended abruptly in early summer 2013 when monsoon rains following the Silver Fire washed ash and fine sediments into Black Canyon eliminating all fishes upstream of the fish movement barrier. Although a number of physical and chemical factors, including displacement by elevated flows, might have contributed to elimination of fishes (Gresswell 1999), it is likely a combination of scoured stream channel in upper-most reaches and deposition of large volumes of fine sediments in middle and lower reaches were major contributors to elimination of fishes, similar to what Rust et al. (2019) reported for upper Rio Grande streams following wildfire and late summer storms.

Following the Silver Fire hatchery-produced Gila trout were released annually in upper Black Canyon and in August 2018 the collection of large numbers of individuals <90 mm TL indicated successful *in situ* spawning and recruitment. In the absence of brown trout, and native warmwater species, it appears Gila trout might establish a viable population in upper Black Canyon. Clearly, native speckled dace, desert sucker, and Sonora sucker could thrive in upper Black Canyon, and it is likely the fourth, longfin dace, could also. What is less certain is whether Gila trout could in the presence of native warmwater fishes. Nonetheless, the results of our study are encouraging in that native warmwater species maintained robust populations and Gila trout maintained mixed size classes, albeit with annual augmentation, in Black Canyon despite the presence of piscivorous brown trout. With brown trout eliminated, we believe that a coexisting warm-coldwater fish assemblage in upper Black Canyon is possible. Other studies (e.g., Dunham et al. 2003; Gido et al. 2019; Jager et al. 2021) have reported the resilience of native fishes to catastrophic wildfire and this study provides yet another example of the resilience of native warmwater species to such events. But this resilience cannot be manifested without connectivity among refugia and depopulated streams, as demonstrated by native warmwater fishes rapidly colonizing depopulated reaches of Black Canyon and the inability of Gila trout to populate Black Canyon without human assistance.

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