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Stream hierarchy defines riverscape genetics of a North American desert fish

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Abstract

Global climate change is apparent within the Arctic and the south-western deserts of North America, with record drought in the latter reflected within 640 000 km² of the Colorado River Basin. To discern the manner by which natural and anthropogenic drivers have compressed Basin-wide fish biodiversity, and to establish a baseline for future climate effects, the Stream Hierarchy Model (SHM) was employed to juxtapose fluvial topography against molecular diversities of 1092 Bluehead Sucker (*Catostomus discobolus*). MtDNA revealed three geomorphically defined evolutionarily significant units (ESUs): Bonneville Basin, upper Little Colorado River and the remaining Colorado River Basin. Microsatellite analyses (16 loci) reinforced distinctiveness of the Bonneville Basin and upper Little Colorado River, but subdivided the Colorado River Basin into seven management units (MUs). One represents a cline of three admixed gene pools comprising the mainstem and its lower-gradient tributaries. Six others are not only distinct genetically but also demographically (i.e. migrants/generation <9.7%). Two of these (i.e. Grand Canyon and Canyon de Chelly) are defined by geomorphology, two others (i.e. Fremont-Muddy and San Raphael rivers) are isolated by sharp declivities as they drop precipitously from the west slope into the mainstem Colorado/Green rivers, another represents an isolated impoundment (i.e. Ringdahl Reservoir), while the last corresponds to a recognized subspecies (i.e. Zuni River, NM). Historical legacies of endemic fishes (ESUs) and their evolutionary potential (MUs) are clearly represented in our data, yet their arbiter will be the unrelenting natural and anthropogenic water depletions that will precipitate yet another conservation conflict within this unique but arid region.

Keywords: Bluehead Sucker, Bonneville Basin, Colorado River, evolutionarily significant unit, Grand Canyon, management unit, microsatellite DNA, mitochondrial DNA, Snake River, Stream Hierarchy Model, STREAMTREE

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Introduction

Climate change is apparent [Intergovernmental Panel on Climate Change (IPCC) 2007], and nowhere are its effects more visible than in two of earth's unique regions: the Arctic (White *et al.* 2010) and the south-western

deserts of North America (Holycross & Douglas 2007). The sensitivities of these regions to greenhouse gas emissions cast them as potential bellwethers for future impacts (*Warning Signs*: Dow & Downing 2007). For example, climate change has altered Arctic topography by first reducing [National Snow & Ice Data Center (NSIDC) 2012] and then mobilizing perennial sea ice, and with multiple effects. It has forged new navigational routes and promoted resource extraction (Nghiem *et al.* 2007), enhanced oceanic productivity (Tremblay *et al.* 2011), unlocked the North-west Passage (Heide-Jørgen-

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sen *et al.* 2011) and politicized wildlife management (Reich 2011).

In south-western North America, unprecedented drought has been equally multifaceted, with vegetation decimated (van Mantgem *et al.* 2009), wildfires provoked (Westerling *et al.* 2006), snow pack diminished (Pederson *et al.* 2011) and run-off curtailed (Barnett *et al.* 2008). Much as in the Arctic, repercussions are severe yet causation is more ambiguous, due largely to a homogenization of greenhouse gas effects on a regional scale (Cayan *et al.* 2010; Seager & Vecchi 2010). In addition, anthropogenic perturbations unrelated to climate (i.e. stream fragmentation, point-source pollution, impoundments and non-native introductions; Sabo *et al.* 2010b) are strongly manifested as well, and they either mask or exacerbate the regional effects of drought. Yet expectations for climate change (Jones 2011) and their impacts on regional biodiversity (Kerr 2011a) are readily proffered and easily accepted, despite the obvious presence of confounding effects (Kerr 2011b). Herein, we posit the necessary proof-of-concept to gauge the magnitude and direction of predicted climate change in the southwest must involve the calibration of standardized, well-defined biodiversity benchmarks against their habitats. This correction will permit managers to define and prioritize biodiversity as a preliminary to the conservation conflicts that will emanate from an increasingly anthropogenic future (Tickell 2011).

In addition, a testable framework will be quite useful in juxtaposing desert stream fragmentation against genetic diversities of native fishes (as a surrogate for biodiversity health). It will also provide the metrics with which to gauge potential future impacts of dewatering (MacDonald 2010) and to evaluate corresponding deterioration of riverine food webs (Sabo *et al.* 2010a). A predictive model would be especially *apropos* for large-scale, basin-level conservation efforts (Abell *et al.* 2008), particularly given the time dependence these often demonstrate. More importantly, a basin-wide benchmark would allow future impacts of climate change to be compared and contrasted against those already recognized in time and space. This in turn would promote human livelihoods and biodiversity conservation at the watershed level (Sabo *et al.* 2010b) and foster its sustainability over a longer temporal scale (Dudgeon *et al.* 2005). Herein we provide this impetus using a previously described conservation model and relevant algorithms to assess natural and anthropogenic impacts on the historical legacy and evolutionary potential of a widespread endemic big river fish in the upper Colorado River Basin of western North America.

Meffe & Vrijenhoek (1988) were prescient in their recognition that fishes are largely constrained to

unidirectional (downstream) dispersal with population structure dictated by riverine distances, particularly in streams with few historical barriers. They developed the Stream Hierarchy Model (SHM) to represent these relatively continuous hydrological connections within a dendritic watershed and to effectively gauge population divergences and degree of isolation as a response to this hierarchy. The SHM is particularly applicable to managed rivers in that impoundments constrain life histories and block historical migration routes for many big river fishes (Waples *et al.* 2008; Osmundson 2011). Dams also fragment suitable habitat (Sabo *et al.* 2010a) and produce smaller, homogeneous patches incompatible for endemics (Poff *et al.* 2007) yet optimal for non-native apex predators (Minckley & Marsh 2009). These anthropogenic stream alterations often generate bottlenecks and promote genetic drift, with genetic divergences inversely related to hydrological distances, particularly when compared to unaltered systems (Douglas & Douglas 2010).

Meffe & Vrijenhoek (1988) tested the SHM using a small native fish (Sonoran Topminnow, *Poeciliopsis occidentalis*) whose gene flow in the Gila River (AZ) conformed to model expectations, prompting their assertion that SHM probably represents fishes in many lotic systems in the southwest. However, native south-western fishes vary from smaller, sedentary and higher elevation (i.e. Sculpin, *Cottus* spp.) to larger, mobile and mainstem species (i.e. Colorado Pikeminnow, *Ptychocheilus lucius*) (Minckley 1991). The generality of SHM can thus be questioned, not only given broad life history diversities of south-western endemics (Minckley & Marsh 2009), but the equally diverse riverine ecosystems within which they reside (Minckley *et al.* 1986).

We evaluated the generality of the SHM using as our focal species a wide-ranging native fish, the Bluehead Sucker, *Catostomus discobolus* (BHS), which is more vagile than the Sonoran Topminnow but less so than other larger-bodied Colorado River fishes. BHS has considerable longevity (Minckley 1991; Douglas & Marsh 1998), allowing the extrapolation of gene flow in this species to other basin-wide endemics more rare in their distributions (Caro 2010). We generated three hypotheses to test whether predictions of the SHM are consistent within the Colorado River (as opposed to the Gila River, a smaller tributary in the Lower Colorado River basin; Douglas *et al.* 1999). These are (i) BHS population structure and gene flow are due to riverine isolation by distance (IBD); (ii) their genetic divergences are significantly greater in mainstem as opposed to tributaries and (iii) populations in anthropogenically altered streams have significantly reduced genetic diversities and increased divergences when compared to those in unaltered reaches.

We applied coalescent and Bayesian analyses of mitochondrial and microsatellite DNAs to infer contemporary vs. historical gene flow and demographic parameters in BHS and to test for the presence of evolutionarily significant units (ESUs) and management units [MUs; where ESUs are recognized as populations with long histories of genetic separation, while MUs currently exchange so few individuals they are demographically independent regardless of past connectivity (Avice 2000)]. These data, and those derived from other imperiled and/or wide-ranging species (Oahey *et al.* 2004; Mock *et al.* 2006, 2010; Douglas & Douglas 2010), provide a contemporary baseline from which to evaluate future climate change in the basin and to weigh historical vs. anthropogenic impacts within a '... resource-depleted landscape compounded by terrifying distances, catastrophic cloudbursts, withering heat and a bizarre beauty allied with death' (Stegner 1981).

Methods and materials

Sampling, DNA extraction and mitochondrial DNA sequence evolution

Catostomidae, subgenus *Pantosteus* (BHS) is characterized by cartilaginous oral scraping ridges encapsulated within broad, disc-shaped lips (Minckley 1991) and is represented by two subspecies: *Catostomus discobolus discobolus* and *Catostomus discobolus yarrowi*. The former is widespread in the Upper Colorado River basin (C1–C24; Fig. 1, Table 1), plus Grand Canyon (C25–C29) and Little Colorado River (LCR) headwaters (C30–C34) of the Lower Colorado River basin. Disjunct populations are found in Bear and Weber rivers of the endorheic Bonneville basin (B1–B3), plus remnants in the Upper Snake River (S1); for simplicity, we refer to these four locations as Bonneville basin. The *C. d. yarrowi* subspecies (C35; Fig. 1, Table 1) is restricted to the Zuni River headwaters (NM), a tributary of the LCR. Anthropogenic impacts have reduced BHS to 45% of its historical range (Bezzerides & Bestgen 2002), such that it is now endangered in New Mexico (Propst *et al.* 2001) and 'of special concern' in Arizona, Colorado, Idaho, Utah and Wyoming.

Fin clips or juveniles were sampled from 1092 specimens across 39 locations ('populations', Fig. 1, Table 1), averaging 28/location (range 10–62, mode = 28). Genomic DNA was extracted with Puregene DNA Purification or Qiagen DNeasy kits. Mitochondrial (mt) DNA ATP8 and ATP6 genes were amplified (Douglas *et al.* 2006), sequenced using BIGDYE [ver.3.1; Applied Biosystems Inc. (ABI), Forest City, CA, USA] and analysed on an ABI Prism 3100 Genetic Analyser. Sequences were aligned manually using SEQUENCHER (Gene Codes, Ann

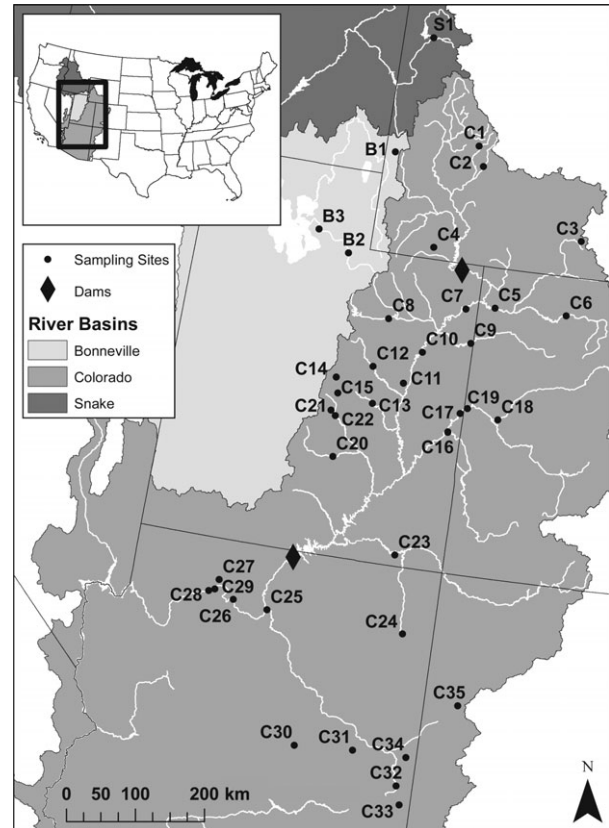


Fig. 1 Sampling locations in three drainage basins of western North America (Colorado River Basin, Snake River Basin and Bonneville Basin) from which Bluehead Sucker (*Catostomus discobolus*) was sampled. Geographic extent of basins is depicted as dark area within the map of the United States (insert, upper left). Sample acronyms are defined in Table 1. Black diamonds represent dams: upper represents Flaming Gorge Dam (UT) on the Green River, while lower represents Glen Canyon Dam (AZ) on the Colorado River.

Arbor, MI, USA) and tested for combination with the partition homogeneity test (Farris *et al.* 1994; Swofford 2001). Sequence evolution was quantified in MODELTEST (Posada & Crandall 1997), and neutrality evaluated in DNASP (Rozas *et al.* 2003) with HKA and MK tests (Hudson *et al.* 1987; McDonald & Kreitman 1991) that contrasted BHS vs. Longnose Sucker (*C. catostomus*, its closest outgroup; Doosey *et al.* 2010). To ascertain clock-like behaviour, we compared BHS vs. outgroup by applying Tajima's (1993) test with five random evaluations per clade (three comparisons each).

Mitochondrial DNA diversity, drainage-level demography and phylogeny

To examine broad-scale regional biodiversity, samples were pooled within drainages and mtDNA sequence divergences (p) calculated among haplotypes, based on

Table 1 Sampling locations and genetic diversity of 1092 *Catostomus discobolus*. Listed are Site = location acronym; letter indicates basin, with S = Snake River, B = Bonneville, C = Colorado River; Location = sampling site; River = major drainage; *n* = sample size; A_R = allelic richness; H_E = mean expected heterozygosity; SD = standard deviation. Evolutionarily significant unit (ESU) and management unit (MU) are defined in Figs 2 to 4.

Site	Location	River	ESU	MU	<i>n</i>	A_R	SD	H_E	SD
S1	Snake River, WY, USA	Snake	1	1	30	5.5	3.0	0.67	0.32
B1	Bear River, WY, USA	Bear	1	1	21	5.1	2.7	0.64	0.30
B2	Weber River (S7), UT, USA	Weber	1	1	34	4.3	2.2	0.59	0.31
B3	Weber River, UT, USA	Weber	1	1	21	5.1	2.2	0.64	0.26
C1	Big Sandy River, WY, USA	Big Sandy	2	3	28	6.4	1.9	0.80	0.12
C2	Little Sandy River, WY, USA	Big Sandy	2	3	17	6.3	1.7	0.80	0.10
C3	Muddy Creek, WY, USA	Little Snake	2	3	23	5.9	2.0	0.74	0.19
C4	Ringdahl Res., WY, USA	Henry's Fork	2	2	33	4.6	1.2	0.72	0.12
C5	Yampa River, CO, USA	Yampa	2	3	28	7.0	1.9	0.82	0.12
C6	Little Yampa Cn., CO, USA	Yampa	2	3	37	7.1	2.0	0.83	0.12
C7	Split Mountain, UT, USA	Upper Green	2	3	16	6.8	2.1	0.79	0.15
C8	Strawberry Res., UT, USA	Duchesne	2	3	28	6.7	2.1	0.82	0.12
C9	White River, UT, USA	White	2	3	10	6.9	2.2	0.83	0.17
C10	Desolation Canyon, UT, USA	Middle Green	2	3	46	6.9	1.9	0.84	0.10
C11	Range Creek, UT, USA	Middle Green	2	3	24	6.1	2.0	0.77	0.15
C12	Price River, UT, USA	Price	2	3	28	7.2	1.7	0.85	0.09
C13	San Rafael River, UT, USA	San Rafael	2	4	30	5.9	1.9	0.76	0.16
C14	Joe's Valley Res., UT, USA	San Rafael	2	4	25	5.7	2.1	0.76	0.15
C15	Millsite Reservoir, UT, USA	San Rafael	2	4	28	5.6	1.9	0.75	0.16
C16	Dolores River, UT, USA	Dolores	2	3	30	6.9	2.1	0.81	0.14
C17	Black Rocks, CO, USA	Upper Colorado	2	3	18	6.7	2.1	0.80	0.13
C18	15-mile reach, CO, USA	Upper Colorado	2	3	26	7.2	2.1	0.83	0.13
C19	West Water Cn, UT, USA	Upper Colorado	2	3	22	7.1	2.0	0.83	0.12
C20	Fremont River, UT, USA	Dirty Devil	2	5	40	6.3	2.1	0.78	0.16
C21	Dirty Devil, UT, USA	Dirty Devil	2	5	46	6.0	2.2	0.76	0.17
C22	Muddy River, UT, USA	Dirty Devil	2	5	25	6.1	2.1	0.77	0.14
C23	San Juan River, UT, USA	San Juan	2	3	30	6.6	2.2	0.81	0.13
C24	Canyon de Chelly, AZ, USA	San Juan	2	6	56	4.2	1.4	0.66	0.15
C25	Little Colorado River, AZ, USA	Lower Colorado	2	7	38	5.4	1.9	0.75	0.15
C26	Shinumo Creek, AZ, USA	Lower Colorado	2	7	62	4.9	1.5	0.73	0.14
C27	Kanab Creek, AZ, USA	Lower Colorado	2	7	21	5.4	1.8	0.74	0.16
C28	Matkatamiba Canyon, AZ, USA	Lower Colorado	2	7	18	5.1	1.8	0.72	0.14
C29	Havasu Creek, AZ, USA	Lower Colorado	2	7	52	4.8	1.4	0.67	0.17
C30	Willow Creek, AZ, USA	Little Colorado	3	8	16	4.7	2.0	0.68	0.18
C31	Silver Creek, AZ, USA	Little Colorado	3	8	19	4.4	1.4	0.68	0.18
C32	Wenima, AZ, USA	Little Colorado	3	8	18	5.7	1.9	0.74	0.16
C33	Nutriosio Creek, AZ, USA	Little Colorado	3	8	10	5.0	1.8	0.68	0.20
C34	East Fork LCR, AZ, USA	Little Colorado	3	8	17	4.8	1.7	0.66	0.21
C35	Agua Remora, NM, USA	Zuni	2	9	21	2.3	1.0	0.36	0.26

1000 bootstrapped replications (MEGA5; Tamura *et al.* 2011). We used 12 outgroups for phylogenetic analyses: (i) Cyprinidae (*Cyprinus carpio*, Carp); (ii) Cobitidae (*Cobitis striata*, Loach, Asia; *Sabanejewia montana*, Central Europe; *S. baltica*, Central Europe); (iii) Catostomidae [Razorback Sucker, *Xyrauchen texanus*; Longnose Sucker, *C. catostomus*; Flannelmouth Sucker, *C. latipinnis*; White Sucker *C. commersonii*; Sonoran Sucker, *C. insignis*; Rio Grande Sucker, *C. plebeius*; Desert Sucker, *C. clarkii*; Mountain Sucker, *C. platyrhynchus* (from this point, common names will be used in text to designate species)].

Data were input to MRBAYES 3.1.2 (BA, Ronquist & Huelsenbeck 2003), with GTR + I + G as the appropriate model (based on MODELTEST). BA involved two runs (five chains each) sampled every 1000 generations and terminated when average standard deviation among split frequencies were <0.001. Parameters and trees were estimated from 20 million generations (less 30% burn-in) and visualized as a majority-rule consensus tree in FIGTREE (ver.1.3.1; <http://tree.bio.ed.ac.uk/software/figtree/>).

Following neutrality tests (above), we computed Tajima's *D* (Tajima 1989) and Fu's F_S (Fu 1997) to infer

demographic histories. The latter is particularly efficient at detecting population expansion, especially when contrasted against F_u and Li's F^* and D^* (Fu & Li 1993). Additionally, we conducted regional mismatch distribution analyses (MDA; Rogers & Harpending 1992), defined as the number of nucleotide differences between all pairs of individuals and employed the R^2 statistic (Ramos-Onsins & Rozas 2002) to assess statistical significance. We derived Tajima's D , Fu's F_s , F_u and Li's F^* and D^* , MDA and R^2 in DNASP using the coalescent with 1000 replications.

Microsatellite DNA diversity and population structure

To quantify contemporary genetic structure and habitat effects, BHS was assessed across 16 fast-evolving microsatellite (msat) DNA loci developed for catostomids (Tranah *et al.* 2001) and cross-amplified in *C. discobolus* (Appendix I). Forward primers were dye-labelled (ABI dye set DS-33). Polymerase chain reactions (PCRs) were run in 10–12 μ L volumes containing Go-*taq* 1 \times flexi buffer (PROMEGA), 2.0 mM $MgCl_2$, 4.2 μ M dNTPs, 4.8 μ g BSA, 0.5 units Go-*taq* DNA polymerase (PROMEGA) and 20 ng DNA. Cycling conditions were as follows: initial denaturation at 95 °C/3 m, 15 cycles for 45 s at 95 °C, 45 s at 52 °C, 1 m at 72 °C, 25 cycles for 30 s at 95 °C, 30 s at 52 °C and 45 s at 72 °C. Fragments were analysed on an ABI (Applied Biosystems, Inc.) Prism 3100 Genetic Analyser along with an internal size standard (Liz500). Alleles were sized with GENESCAN v3.7, scored with GENOTYPER v3.7 (ABI) and evaluated for null alleles/scoring errors using MICROCHECKER v2.2.3 (van Oosterhout *et al.* 2004).

Deviations from Hardy–Weinberg (HW) and linkage equilibria (LD) were computed using exact tests in GENEPOP '007 (Rousset 2008), with P -values estimated via Markov Chain with 10 000 dememorizations, 200 batches, 5000 iterations and Bonferroni-adjusted $\alpha = 0.0031$. Expected (H_E) and observed (H_O) heterozygosities, number of alleles and private alleles/population and/locus were calculated in GENALEX v6.1 (Peakall & Smouse 2006). Allelic richness was estimated using rarefaction based on the smallest diploid sample ($n = 20$; HP-RARE, Kalinowski 2005).

Assignment tests were conducted in STRUCTURE (Pritchard *et al.* 2000, 2009) to determine the number of distinct gene pools. Simulation parameters were 'admixture' and 'allele frequencies correlated among populations'. Exploratory analyses had burn-in = 100 000, chain length = 200 000, with highest posterior probabilities for clusters at $k = 9$ –12. Subsequent runs focused on these values, with each k replicated 10 \times with burn-in/chain lengths extended to 200 000 and 500 000, respectively. Redundant runs were conducted in that large

and complicated data sets (as herein) can collapse onto multiple values, particularly when 'admixture' is applied (Waples & Gaggiotti 2006). To determine divergences among locations and STRUCTURE-defined clusters, we calculated pairwise F_{ST} estimates (Goudet 1995) and 95% bootstrap confidence intervals. The G -based Fisher's exact test was applied in GENEPOP, with parameters previously mentioned and with Bonferroni-adjusted significance.

Stream hierarchy, population dynamics and MUs

To estimate hierarchical structure in drainages and basins and, thus, to test the SHM, we assessed spatial variance in allele frequencies with a locus-by-locus analysis of molecular variance (AMOVA; Excoffier *et al.* 1992; Michalakis & Excoffier 1996), as implemented in ARLEQUIN v3.1 (Excoffier *et al.* 2005) and with variance partitioned across basins. We applied a Mantel test and 1000 permutations (IBD V1.52; Bohonak 2002) to examine IBD by comparing genetic distance (i.e. $F_{ST}/1 - F_{ST}$; Rousset 1997) vs. river distance (in km) as geo-referenced in ARCGIS 9 \times (ESRI) among our 35 Colorado River locations (excluding Bonneville Basin; S1, B1–B3).

The SHM stresses stream networking as important in shaping patterns of genetic diversity. We inferred relative genetic distances for each stream section based on pairwise (among-site) chord distances (Cavalli-Sforza & Edwards 1967) mapped onto stream sections identified following the methods implemented in STREAMTREE (Kalinowski *et al.* 2008). The latter differs from IBD in that it allows shorter sections of streams to be assigned larger genetic distances and does not involve geographic distance but rather stream network topology. This approach can also isolate particular sections of a network that can disrupt IBD (such as barriers or corridors). STREAMTREE compared the mid-point-rooted neighbour-joining (NJ) tree against the actual stream network via the coefficient of determination (R^2) from linear regression. Bonneville basin (S1, B1–B3) was excluded from the analysis, given its long isolation from the Colorado River basin (Minckley *et al.* 1986).

The SHM predicts that populations within smaller, headwater streams will bottleneck and diverge significantly when connectivity is disrupted by impoundments, particularly when compared to populations in unobstructed streams. To detect recent bottlenecks [i.e. within $4N_e$ generations], we contrasted excess vs. expected heterozygosity at equilibrium using the Wilcoxon signed rank test in BOTTLENECK (Piry *et al.* 1999). Infinite allele (IAM) and two-phase (TPM) models were run for 1000 iterations, with the latter more appropriate as it permits multirepeat mutations in allele size. TPM

parameters were 90% of loci conforming to SMM and default variance = 30. Significance for two-tailed tests (heterozygote excess/deficiency) were assessed at Bonferroni-adjusted $\alpha = 0.0031$. Only significant deviations under both models were considered as a true signal.

The SHM predicts stream fragmentation will reduce population sizes and elevate genetic divergences above impoundments, especially when compared to unimpeded streams. To test for potential divergences among smaller, more peripheral populations above barriers, we estimated effective population sizes (N_e) of STRUCTURE-defined clusters using a one-sample LD estimator (LDNE; Waples & Do 2008). LDNE produces largely unbiased estimates of N_e under a wide range of sample sizes and true N_e values, and after excluding alleles with frequencies less than a range of critical values (i.e. $P_{crit} = 0.05, 0.02$ and 0.01).

Previously, MUs have been characterized by significant differences in allele frequencies, as gauged by a comparison of pairwise F_{ST} values. This approach has recently been amended to include contemporary dispersal rates, such that MUs are now defined by demographic independence (i.e. genetic divergence approximating a dispersal rate <10%, Palsbøll *et al.* 2006). We employed BAYESASS 3 (Wilson & Rannala 2003) to estimate migration rates for our STRUCTURE-derived groupings, using 10 million iterations (1 million discarded as burn-in) and 1000 iterations between MCMC sampling. Mixing parameter for allele frequencies, inbreeding coefficients and migration rates were iteratively adjusted so as to accrue acceptance rates of 25%, 28% and 30%, respectively (where values between 20% and 40% are deemed optimal).

Results

Mitochondrial DNA divergence, demography and phylogeny

Sequence analysis was performed on the combined ATP8 and ATP6 genes across a subset of 495 samples (averaging 13/location, range 4–33, mode = 8) and resulted in 836 bp coalesced into 65 haplotypes (43 ingroup + 20 outgroup). Combining mtDNA sequences was supported by a nonsignificant partition homogeneity test (Paup*: $P > 0.25$). All sequences were evolving neutrally [HKA: (0.85 < $P < 0.98$), MK: (0.82 < $P < 0.96$)] and in a rate-uniform manner (Tajima’s test, $P > 0.53$).

Our BA tree (Fig. 2), rooted at Carp, depicts Cobitidae as basal to Catostomidae, with Longnose Sucker placed as sister to its congeners. Next is a clade consisting of White and Utah suckers and a cluster composed of Razorback, Sonoran and Flannelmouth. Within *Pantosteus*, BHS is split into three clades (ESUs): ESU-1

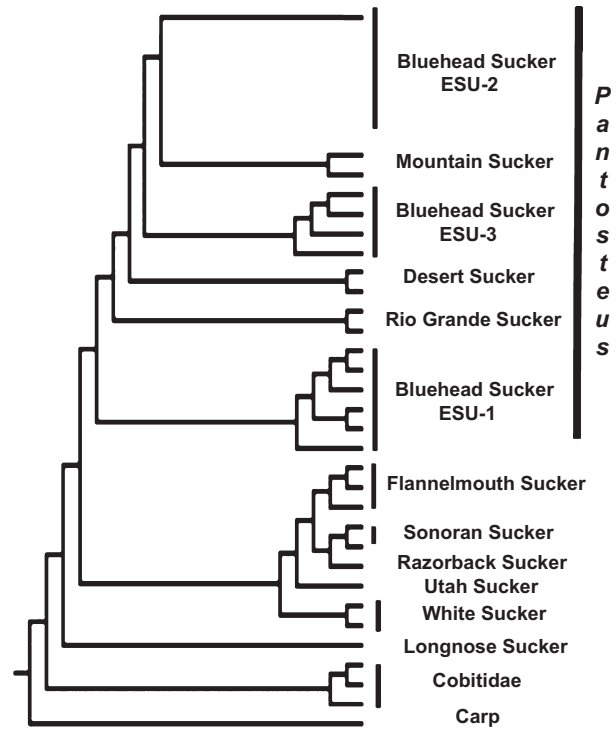


Fig. 2 Majority-rule (MR) consensus tree (3050 trees) derived from a Bayesian analysis of haplotypes spanning 836 bp of ATPase 8 and ATPase 6 mitochondrial DNA across 43 Bluehead Sucker (BHS) (*Catostomus discobolus*) and 20 outgroups {Carp (*Cyprinus carpio*); Family Cobitidae; Longnose Sucker (*Catostomus catostomus*); White Sucker (*Catostomus commersonii*); Utah Sucker (*Catostomus ardens*); Razorback Sucker (*Xyrauchen texanus*); Sonoran Sucker (*Catostomus insignis*); Flannelmouth Sucker (*Catostomus latipinnis*); Rio Grande Sucker [*Catostomus (Pantosteus) plebeius*]; Desert Sucker [*Catostomus (Pantosteus) clarkii*]; Mountain Sucker [*Catostomus (Pantosteus) platyrhynchus*]}. All nodes are at 100%. Three evolutionarily significant units (ESUs) are indicated.

comprising Bonneville Basin/Snake River, ESU-2 representing Colorado River Basin, except Upper LCR, which forms ESU-3 (Table 1). The Zuni Sucker subspecies (*C. d. yarrowi*) was not distinct, but shared a common haplotype with ESU-2. Interestingly, ESU-1 is basal to all other *Pantosteus*, followed by Rio Grande Sucker, Desert Sucker and ESU-3 as sister to a clade containing Mountain Sucker and ESU-1.

Sequence divergence (Table 2) ranged from 0.1% (± 0.1) between BHS-subspecies to 1.7% (± 0.4) between BHS-ESUs. Within the subgenus *Pantosteus*, two species scarcely diverged from BHS, with Desert Sucker at 1.0–1.6% (± 0.4) and Mountain Sucker at 0.0–1.1% ($\pm 0.0–0.3$); only Rio Grande Sucker was clearly distinct at 4.4–5.9% (± 0.7). In comparison, divergence between subgenera *Pantosteus* and *Catostomus* was on average 4.4% and 6.7% within *Catostomus*.

Table 2 Sequence divergence (%) across 836 bp of mtDNA ATP-6 and ATP-8 genes within and among Bluehead Sucker (BHS = *Catostomus discobolus*) and other catostomid species. Lower triangle represents pairwise sequence divergence, and upper triangle shows standard errors. Bayesian Analysis identified three ESUs in BHS (Fig. 2) with ESU-1 = Bonneville Basin/Snake River; ESU-2 = Colorado River Basin and ESU-3 = Little Colorado River; ZUN = *Catostomus discobolus yarrowi* subspecies in Zuni River (NM). Other species in the subgenus *Pantosteus* are MTS = Mountain Sucker (*C. platyrhynchus*); DES = Desert Sucker (*C. clarkii*) and RGS = Rio Grande Sucker (*C. plebeius*). Outgroups are FMS = Flannelmouth Sucker (*C. latipinnis*); SOS = Sonoran Sucker (*C. insignis*); WHS = White Sucker (*C. commersonii*); UTS = Utah Sucker (*C. ardens*) and LNS = Longnose Sucker (*C. catostomus*)

<i>Pantosteus</i>												
	ESU-1	ESU-2	ESU-3	ZUN	MTS	DES	RGS	FMS	SOS	WHS	UTS	LNS
ESU-1		0.003	0.004	0.004	0.003	0.004	0.007	0.010	0.010	0.009	0.010	0.010
ESU-2	1.1		0.004	0.001	0.000	0.004	0.007	0.010	0.010	0.009	0.010	0.010
ESU-3	1.7	1.2		0.004	0.003	0.004	0.007	0.010	0.011	0.009	0.011	0.010
ZUN	1.3	0.1	1.3		0.001	0.004	0.007	0.010	0.010	0.009	0.010	0.010
MTS	1.1	0.0	1.1	0.2		0.003	0.007	0.010	0.010	0.009	0.010	0.010
DES	1.2	1.0	1.6	1.2	0.9		0.007	0.010	0.010	0.009	0.010	0.010
RGS	4.9	4.4	5.0	4.6	4.4	4.8		0.011	0.011	0.010	0.011	0.010
FMS	8.7	9.0	9.8	9.2	9.0	8.9	11.0		0.006	0.007	0.005	0.010
SOS	9.2	9.3	10.0	9.4	9.3	9.3	10.6	3.2		0.008	0.007	0.010
WHS	8.1	8.0	8.7	8.1	8.0	8.1	10.4	5.6	5.8		0.007	0.009
UTS	9.0	9.2	10.0	9.4	9.3	8.7	12.0	2.7	4.1	4.8		0.010
LNS	10.0	10.0	10.5	10.1	10.0	9.7	11.7	10.1	10.9	8.9	10.4	

Strong population expansion was recorded only for ESU-2, as indicated by significant negative statistics (Tajima's $D = -2.015$, $P < 0.006$; Fu's $F_S = -43.938$, $P < 0.0000$; Fu and Li's $F^* = -2.872$, $P < 0.012$; Fu and Li's $D^* = -2.64$, $P < 0.018$). MDA, another approach to assess historical changes in population size, reaffirmed the rapid demographic expansion of ESU-2 with observed values in a unimodal plot significantly displaced from expected ($R^2 = 0.043$; $P < 0.0000$). The remaining two ESUs also had negative (but nonsignificant) values for the above statistics, while the multimodal MDA plot for ESU-1 suggested a population at constant size.

Microsatellite diversities, divergences and population structure

All 16 loci were polymorphic, averaging 32.6 alleles (range 10–57; Appendix I). Significant deviations from HWE occurred in only 2.85% tests (i.e. 12 of 420). Significant LD occurred in 11.66% of comparisons (49 of 420), with 33 attributable to Havasu Creek (C29). Once this population was removed from analyses, the 16 remaining significant tests were less than the 21 expected by chance alone ($\alpha = 0.05$), indicating HWE and LD would not impact further analyses. Additionally, MICROCHECKER revealed potential null alleles in nine populations (of 39; 23%). However, three (9%) were at one locus (Dlu233), two (6%) at another (Dlu4153), with one population (C12) showing evidence for null alleles at both loci, accounting for seven of nine occurrences

(78%). No locus-specific patterns were detected in the remaining four tests.

Genetic diversity within BHS populations (Table 1) was moderate to high, with allelic richness (adjusted for sample size) ranging from 2.3 (SD = 1.0) to 7.2 (SD = 1.7) and H_E varying from 0.36 (SD = 0.26) to 0.85 (SD = 0.09, Table 1). Among ESUs, populations in ESU-2 showed higher mean allelic richness ($A_R = 6.0$, SD = 0.0) and heterozygosity ($H_E = 0.76$, SD = 0.09) than those in ESU-1 ($A_R = 5.0$, SD = 0.5; $H_E = 0.64$, SD = 0.03) and ESU-3 ($A_R = 4.9$, SD = 0.5; $H_E = 0.69$, SD = 0.03). The population representing *C. d. yarrowi* was characterized by very low genetic diversity ($A_R = 2.3$, $H_E = 0.36$). Genetic divergence was variable among populations with F_{ST} at 0.0–0.45 (0.1–0.17 CI) and greatest for *C. d. yarrowi* (C35) vs. any other population ($F_{ST} = 0.32$ –0.45). As expected, pairwise F_{ST} values were elevated between populations from different ESUs, but surprisingly low among populations in ESU-1 ($F_{ST} = 0.07$ –0.08). AMOVA identified 14.3% of genetic variation among basins, 9.0% among populations within basins and 76.7% within populations.

STRUCTURE runs using all locations plateaued at $k = 9$, remained stable through $k = 11$, then decreased through $k = 14$. At $k = 11$, three clusters within mainstem populations in the Green and Upper Colorado rivers reflected high levels of admixture and ill-defined separation. Relationships among genetic vs. geographic distances were nonsignificant ($Z = 2.54 \times 10^{13}$; $r = 0.03$; $P = 0.28$). Based on these results, we grouped populations into nine clusters, considered MUs (Fig. 3), with

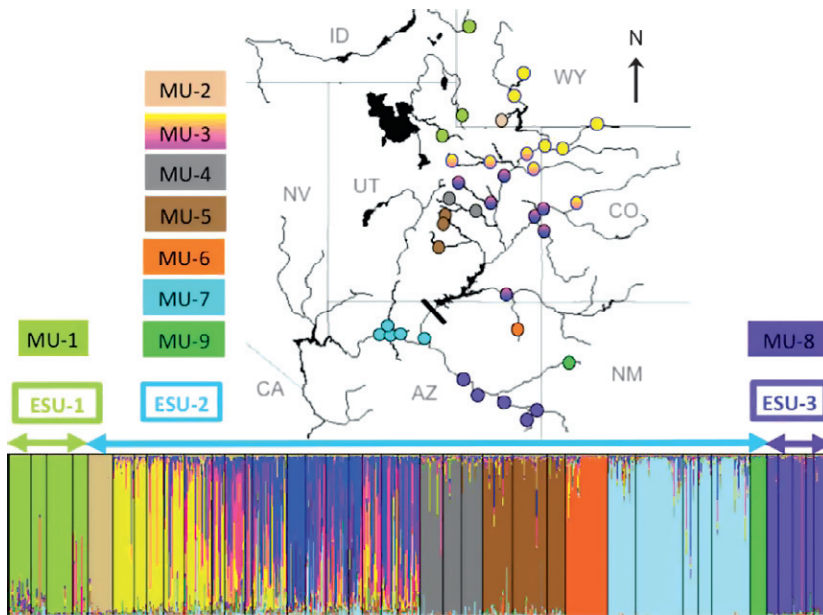


Fig. 3 Management units (MUs) identified via assignment test of 1092 Bluehead Sucker [*Catostomus (Pantosteus) discobolus*] genotypes derived from 16 microsatellite DNA loci. Bar plot depicts assignment of individuals to gene pools (colours) derived from STRUCTURE. Map shows geographic distribution of 9 MUs, with sampling site reflecting gene pool colour. MU-1 (green) = Bonneville Basin/Snake River; MU-2 (light brown) = Ringdahl Reservoir; MU-3 (yellow-to-blue = Green/Colorado River; MU-4 (grey) = San Rafael River; MU-5 (dark brown) = Dirty Devil River; MU-6 (orange) = Canyon de Chelly; MU-7 (light blue) = Grand Canyon; MU-9 (bright green) = Zuni River; MU-8 (purple) = Little Colorado River. Evolutionarily significant units (ESUs) that contain the MUs are also designated. See Table 1 for detailed information on sampling sites.

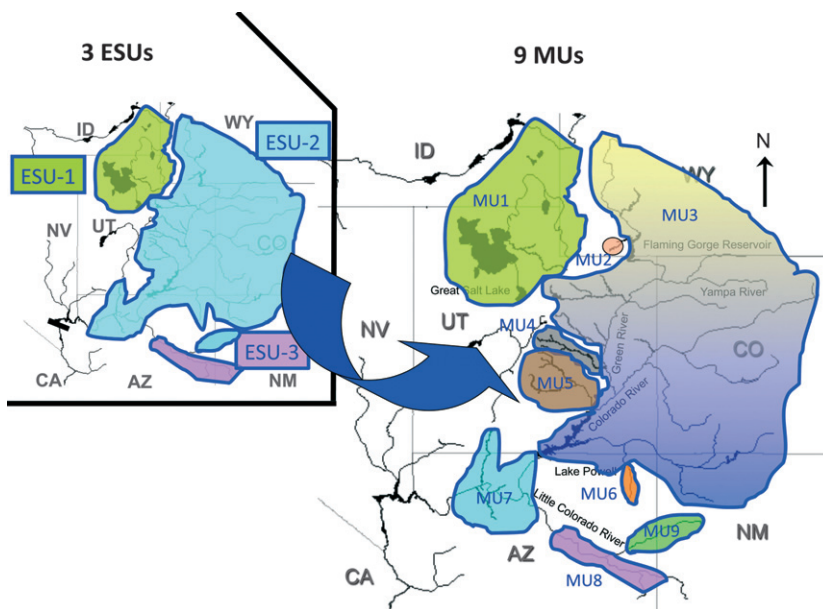


Fig. 4 Geographic distributions of three evolutionarily significant units (ESUs) and nine management units (MUs) in Bluehead Sucker (*Catostomus discobolus*). ESUs (left) were derived from 836 bp of ATP-8 and ATP-6 mitochondrial DNA genes. ESU-1 (green) = Bonneville Basin/Snake River; ESU-2 (blue) = Colorado River; ESU-3 (purple) = Upper Little Colorado River. Two MUs (right) correspond to ESUs (ESU-1 = MU-1, ESU-3 = MU-8), whereas ESU-2 subdivides into seven MUs (MU-2 through MU-7, and MU-9). See Table 1 for detailed information on ESUs and Figure 3 for MUs.

Green/Upper Colorado rivers combined to reflect their admixture (Fig. 4). Structure-defined clusters were further supported by pairwise F_{ST} values, with the lowest (0.02) between Green/Yampa rivers vs. Upper Colorado River mainstem, again suggesting a single cluster.

Stream networks, effective population sizes and migration rates among MUs

Genetic distances among sample locations (populations) were significantly related to the stream segments sepa-

rating them, with results depicted in a plot of expected vs. observed distances fitted to the river network for each stream section between sampling locations (STREAMTREE, Fig. 5; $R^2 = 0.987$). Average mainstem distance = 0.006, with an 8.5 \times -differential for each section entering the tributaries ($d = 0.051$). Interestingly, genetic distances for eight (of 20) mainstem sections (i.e. 40%) approximated zero, as predicted by the SHM. Eleven (of 18) streams entering tributaries (i.e. 61%) averaged >0.01 (range 0.0–0.29), further demonstrating that topology significantly influences population structure of Colorado River Basin BHS. Seven populations [i.e. C04

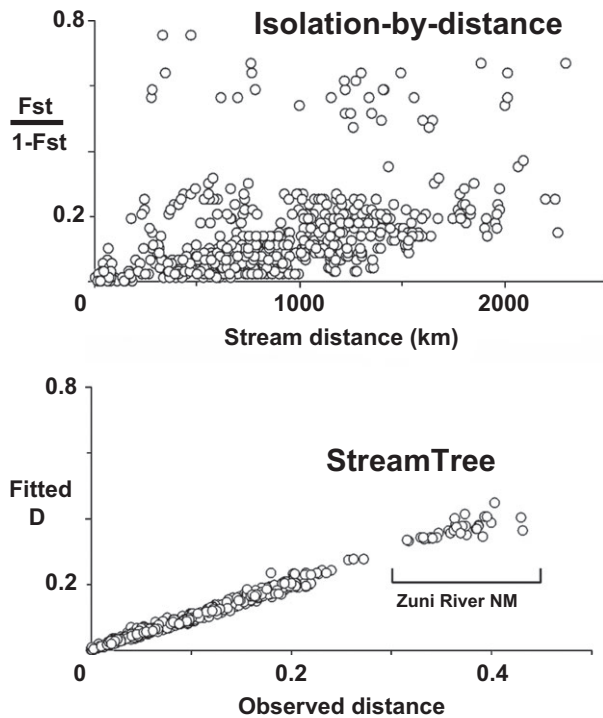


Fig. 5 Plots depicting results produced by analyses of isolation-by-distance (IBD: top) and STREAMTREE (bottom). The IBD plot contrasts genetic distances (x-axis) against pairwise stream distances in km ($r = 0.03$). The STREAMTREE plot depicts expected genetic distances (x-axis) vs. observed distances, fitted to the river network for each stream section between sampling locations ($R^2 = 0.987$). Bracketed data in the STREAMTREE plot are pairwise comparisons among *Catostomus discobolus yarrowi* (Zuni River, NM; Table 1) and all other locations.

(Ringdahl Res., WY), C30, C31 (Willow and Silver cks. AZ), C11, C12 (Range Ck. and Price River, UT, USA), C24 (Canyon de Chelly, AZ, USA) and C35 (Agua Remora, NM, USA)] were highly differentiated when compared with those in close geographic proximity or within the same catchment, a result counter to the assumptions of IBD (Kalinowski *et al.* 2008). In fact, the IBD plot (Fig. 5) demonstrates a compendium of smaller stream distances associating with larger genetic distances, and vice-versa, contributing to the nonsignificant relationship. STREAMTREE results also supported those from STRUCTURE, with upper Colorado/Green rivers being admixed, whereas tributaries reflect distinct gene pools. These data reject our second hypothesis (i.e. genetic diversity is significantly greater in mainstem vs. tributary populations). Additionally, there is no evidence that dams altered historical population structure in this region of the basin, other than that for Ringdahl Reservoir.

Across all 39 populations, seven showed significant genetic bottlenecks (within $4N_e$ generations) under

Table 3 Estimates of gene flow calculated for nine management units (MUs) in Bluehead Sucker (*Catostomus discobolus*). Parameters are Migration = migration rate (standard error); N_e = LNDE effective population size with 95% confidence intervals (CI) and inbreeding coefficient F_{IS} (with standard error). For details on MUs, see Table 1 and Fig. 3

MU	Migration	N_e	95% CI	F_{IS}
MU-1	0.95 (0.01)	76	58.1–102.3	0.07 (0.013)
MU-2	0.93 (0.02)	120	37.3–∞	0.11 (0.022)
MU-3	0.96 (0.01)	742	562.1–1056.8	0.05 (0.005)
MU-4	0.96 (0.01)	351	192.4–1403.6	0.03 (0.011)
MU-5	0.97 (0.01)	710	310–∞	0.02 (0.008)
MU-6	0.96 (0.01)	39	27.4–57.8	0.16 (0.021)
MU-7	0.95 (0.01)	90	76.7–107.7	0.05 (0.009)
MU-8	0.94 (0.02)	20	17–23.3	0.17 (0.015)
MU-9	0.91 (0.03)	10	2.9–35.6	0.55 (0.031)

either the infinite alleles (IAM) or two-phase model (TPM). However, only one (C35) was significant for both (IAM, $P = 0.00002$; TPM, $P = 0.00168$). Genetic bottlenecks were also evaluated for each of the nine MUs (Table 3), and N_e ranged from 9.7 in MU-9 to 742 in MU-3. All 95% confidence intervals had discrete upper/lower bounds, except for MU-5 and MU-2, which had upper intervals of infinity, a known weakness of N_e LD estimators (Beebe 2009). All MUs displayed migration rates <9.7%, as calculated in BAYESASS 3. Inbreeding ($F_{IS} = 0.55$) was also evident in MU-9, representing the *C. d. yarrowi* subspecies.

Thus, we cannot reject the hypothesis that populations in anthropogenically altered streams have significantly reduced genetic diversities and increased divergences when compared to those in unaltered reaches. Most dams in western North America were built in the early to mid-20th century, and Ringdahl Reservoir (C04, Table 1; MU-2, Table 3) represents one of the few known BHS populations existing within such an impoundment. It displays reasonable values for N_e (120) and F_{IS} (0.11), yet lacks any capacity for natural immigration. These factors increase its value from a management standpoint in that existing barriers prevent the invasion of introduced non-native suckers, whereas resident BHS may serve as a source for translocation, supplementation or broodstock establishment.

Discussion

Range shifts are a by-product of climate change (Mair *et al.* 2012; Merilä 2012), and while their effects can be mitigated through conservation planning, the latter has been primarily terrestrial in its focus (Thomas 2010), possibly due to the limited surface area displayed by global freshwater systems (i.e. 0.8%; Dudgeon *et al.*

2005). Despite this, freshwaters encompass *c.* 6% of all described biodiversity (Dudgeon *et al.* 2005), support riparian zones, adjacent terrestrial reaches, upstream dendritic networks, larger, more expansive downstream reaches (i.e. an extensive 'riverscape'; Fausch *et al.* 2002) and also represent a contemporary focus for global sustainability (i.e. UN 'Water for Life' Decade, 2005–2015; <http://www.un.org/waterforlifedecade/background.shtml>). Similarly, a second focus for global sustainability are the global deserts and their accompanying drought (i.e. UN 'Decade for Deserts and Desertification', 2010–2020; <http://unddd.unccd.int/>). Both are uniquely juxtaposed within south-western North America (deBuys 2011), a region with relentlessly persistent drought (Ross 2011) and unprecedented anthropogenic water use (Romm 2011). Yet the cumulative impacts of these drivers on native fish biodiversity remain surprisingly obscure, a possible result of traditional assay methods coupled with limited baseline data. Here, we tested the predictive power of a conservation tool (SHM) to manage endemic fish biodiversity within a large freshwater desert system by juxtaposing stream hierarchy against historical and contemporary genetic diversities in a surrogate endemic (the BHS).

Mitochondrial DNA diversity within and among basins and the delineation of ESUs

Our first step in prioritizing basin-level conservation efforts was to establish historical relationships and connectivities among drainages. First, we evaluated mtDNA sequence divergences within and among species of catostomids (Table 2). Our analyses revealed clear distinction between *Catostomus* (*sensu stricto*) and the subgenus *Pantosteus*, but relationships within the latter were surprising. Within-species divergences were often larger than those among-species, suggesting the potential for unrecognized biodiversity. While BHS was clearly distinct from Rio Grande Sucker, it was quite similar to both Desert and Mountain suckers. The latter is difficult to distinguish phenotypically from BHS, particularly as juveniles, and the two species readily hybridize (Smith 1966). Low divergence could reflect misidentification, hybridization or incomplete mtDNA lineage sorting. Additionally, Desert Sucker and BHS are ecological equivalent sister species in the lower and upper Colorado River basins, respectively.

Intraspecific lineages with separate evolutionary trajectories are often designated as ESUs, a distinction particularly important for declining species or those shrinking in distribution. ESUs were originally defined as being reciprocally monophyletic with regard to mtDNA and with significant divergence at nuclear loci

(Moritz 1994). This definition (as followed herein) is objective and unambiguous, whereas others that invoke the necessity of 'adaptive variation' are deemed less so (Holycross & Douglas 2007). We identified three ESUs within BHS (Fig. 4), based on mtDNA clades (Fig. 2), microsatellite analysis (Fig. 3) and the SHM. Our take-home message (also amplified with MUs below) is that molecular divergences among endemic fish populations often juxtapose quite well with drainage histories and with their concomitant stream hierarchies.

In this sense, it was reassuring to identify two basins (Colorado River and Bonneville/Snake River) as ESUs, particularly given the availability of ample hydrological evidence (Minckley *et al.* 1986). On the other hand, recognition of the upper LCR as a distinct ESU seemed curious in a contemporary sense as this drainage is a free-flowing tributary of the mainstem Colorado River. However, it was completely blocked by volcanism at various times in the past, with the most recent (at 20 kya) forming a spectacular 56-m cataract termed 'Grand Falls'. Other blockages occurred earlier (2.4 and 0.5 mya) and farther downriver (30 and 80 km) but have subsequently eroded (Duffield *et al.* 2006).

Population structure within and among basins and the delineation of recent diversity

Movement patterns and gene flow are largely unknown for south-western native fishes, and BHS is no exception, with ecological studies focusing instead on community responses to anthropogenic disturbance (Propst & Gido 2004). However, estimates of gene flow and population connectivity, as derived from neutral molecular markers, provide excellent data on movement patterns (Douglas & Douglas 2010) and were used herein to delineate 9 MUs. Two of these corresponded to ESUs: the Bonneville Basin ESU-1 (MU-1) and upper LCR ESU-3 (MU-8), respectively. The seven remaining MUs represent distinct gene pools within the Colorado River basin. The presence of low (<9.7%) migration rates (Palsbøll *et al.* 2006) supports the validity of these MU designations and provides an hierarchical population structure from which to develop a basin-wide adaptive management programme.

The processes that shaped biodiversity must be understood before long-term conservation goals can be implemented and managed. While direct causation cannot be determined for evolutionary events, correlation can be informative. For example, two MUs within the Colorado River basin associate well with geomorphology. One, the Grand Canyon (MU-7), is a World Heritage Area and one of the largest geomorphic features of the globe. Its evolution is controversial, particularly

with regard to the Colorado River, which only became a unified (subcontinental) drainage system *c.* 5 mya (Wernicke 2011). It was subsequently dammed above Grand Canyon in 1962 (Douglas & Marsh 1996, 1998; Fig. 1). Canyon de Chelly (MU-6) represents a second canyon-defined MU, but within a National Monument entirely on Navajo Nation Tribal Trust Land. Its waters run west through steep-walled canyons from the Chuska Mountains (Arizona–New Mexico) to the San Juan River, then west to the Colorado River (Fig. 1). Both Grand Canyon and Canyon de Chelly are topographically distinct, and their resident BHS reflect low gene flow and concomitant genetic divergences.

Two additional MUs were defined as tributary populations of the Colorado River (Fig. 4), with hydrological processes again offering a plausible explanation for their distinctiveness. Headwaters of the Dirty Devil (MU-5) and San Rafael rivers (MU-4) are west of the Colorado River upstream of Grand Canyon (Fig. 3), with their isolation a result of steepening gradients as their confluences retained a connection to a rapidly incising mainstem (Cook *et al.* 2009). The hydrographical isolation of these tributaries is reaffirmed by extensive morphological variation in resident BHS (Smith 1966) and, when coupled with their tolerance for lower temperatures and higher gradients compared to other Colorado River fishes, allows for persistence in higher-elevation streams.

Population bottlenecks, clines of admixture and dispersal from refugia

Our primary focus was to quantify intraspecific genetic variation as a means of describing BHS population structure and identifying hierarchical regions in the Colorado River and adjacent basins based on molecular divergence. However, (as before) historical population demography should be considered before MUs can be correctly adjudicated.

Intraspecific diversity has been recognized in BHS, with *Catostomus discobolus yarrowi* identified as a subspecies in the Zuni River (C35). Smith (1966) originally suggested *C. d. yarrowi* was a hybrid between *Catostomus discobolus discobolus* and Rio Grande Sucker whereas Crabtree & Buth (1987) argued for nonhybrid distinctiveness. With regard to mtDNA, *C. d. yarrowi* is indistinguishable from ESU-2 and does not share haplotypes with Rio Grande Sucker. In fact, it is as divergent from the latter as are other BHS (Table 2). Microsatellite analysis identified this population as a distinct gene pool (MU-9), but our results are based on a single population, and we thus consider them tentative. Furthermore, low genetic diversity (Table 1), a small N_e , an elevated F_{IS} (Table 3) and a likely bottleneck within the

last $0.5 - 4N_e$ generations suggest a founder event with subsequent genetic drift. Subspecific designations, particularly when used as biodiversity surrogates, can often dilute management efforts (Holycross & Douglas 2007), and *C. d. yarrowi* may fall within this category.

Our results also indicate considerable admixture within the Green and upper Colorado rivers. The northernmost Colorado River Basin population (C1, Fig. 1) still reflects connectivity with downstream populations despite a truncation of gene flow resulting from the 1964 construction of Flaming Gorge Dam (Fig. 1). Individual BHS can live 20+ years, yielding generations that overlap and thus potentially sustaining a semblance of genetic continuity. Lippé *et al.* (2006) found similar results when investigating a highly endangered eastern North American catostomid (i.e. *Moxostoma hubbsi*). In this sense, long generation time might be a life history strategy in endemic western North American fishes that promotes environmental resilience while minimizing genetic divergences.

The Colorado River Basin ESU also displayed a signature of historical population expansion, a pattern similarly reported in Flannelmouth Sucker (a big river endemic broadly sympatric with *C. discobolus*). These results were attributed to a massive early Holocene drought that forced upper basin mainstem fishes into lower-basin refugia (Douglas *et al.* 2003). When the climate stabilized and the upper basin again became fluvial, Flannelmouth Sucker recolonized upriver but with a genetic signature reflecting founder events and an expansion from Grand Canyon. Given their proclivity for colder water and faster current, upper Colorado River Basin BHS may have been one of few endemics to survive such an event within multiple, high-elevation refugia. Identification of distinct BHS gene pools (MUs) within the Colorado River ESU is congruent with this hypothesis.

Stream hierarchy, biodiversity conservation and implications for management

The management of large watersheds is difficult in that physical size often overwhelms realistic goals, particularly so with the Colorado River Basin, the core watershed and most heavily managed river in southwestern North America (i.e. 640 000 km², seven US and two Mexican states; Kammerer 2005). It drains an arid and resource-poor region (Sabo *et al.* 2010b) yet supports urban centres with the greatest *per capita* water consumption (McCabe *et al.* 2010) and most rapid population growth in North America (Ross 2011; Wu *et al.* 2011), hence its recognition as an exceptional but critically endangered large river (Beaumont *et al.* 2011). Numerous state/federal management agencies monitor

its biodiversity to determine whether legal, regulatory and policy objectives have been achieved and, to do so, rely upon distributional and spatial data from catch/release efforts. However, the fine-grained watershed-scale perspective needed for adaptive management should instead employ as a monitoring emphasis the application of molecular genetic data (Douglas & Douglas 2010).

In this study, the SHM was used to predict population structure of endemic fishes in the Colorado River Basin, with visualization supplied by STREAMTREE (Fig. 5) under the supposition that BHS is an adequate surrogate species for the Colorado River ecosystem. Numerous opinions have emerged regarding surrogacy (Rodrigues & Brooks 2007; Caro 2010), yet questions remain. For example, surrogacy has a broad interpretation, to include 'environmental' (i.e. use of contextual data such as species assemblages or abiotic information to represent a subset of target species) vs. 'species' [i.e. extent to which a surrogate (or a set) represents a target]. We support our position by noting BHS is a conservation target in its own right, with a tacit assumption that efforts to conserve it will also effectively protect other endemics. In addition, practical conservation planning based on the population structure of well-known taxonomic groups is valid under the assumption that the evolutionary histories of less well-known taxa are captured as well. The most effective (i.e. least expensive) way to do so is by maintaining native species in habitats with the greatest probability of success. This juxtaposes with more controversial opinions regarding conservation triage (i.e. retention of pattern or process, as balanced by need vs. cost effectiveness; Arponen 2012).

The necessity of quantifying anthropogenic impacts (e.g. fragmentation, dewatering, impoundment and pollution) as a baseline for contemporary climate change in south-western North America is indeed imperative. Climate-mediated and region-specific projections are controversial (Jones 2011), ranging from dire (Balling & Goodrich 2010) to benign (Gao *et al.* 2011). Given this, a testable model to juxtapose genetic diversity of native fishes against stream fragmentation will provide the quantitative baseline against which potential climate-mediated impacts of dewatering can be gauged (MacDonald 2010). This relationship can be broadened, extended and translated to regions less well monitored, with the caveat that precipitation projections will remain uncertain and that regions and models are key factors (Kerr 2011b). Our results also argue for the protection of specific drainages or basins, particularly those that contain ESUs and MUs for one or more key species. In our study, three ESUs and nine MUs within BHS provide a formidable blueprint for biodiversity

conservation in the Colorado River and Bonneville basins.

Our results also support an argument that rapid habitat depletion (Holycross & Douglas 2007), reduced gene flow (Douglas *et al.* 2003) and presence of MUs (herein) retard the capacity of endemic biotas to withstand global change, particularly under the assumption that rapid change will overwhelm the capacity of most populations and species to adapt (Schloss *et al.* 2012). Given this, how should biodiversity be managed in the Colorado River ecosystem? Clearly, we must retain both pattern (significant divergences among/within basins) and process (MUs within basins), particularly because the species within which these are found represent the most endemic of North American freshwater fishes (Fig. 2c in Abell *et al.* 2008). These aspects can only be achieved through close collaboration with federal, regional and state water administrations and by applying a quantifiable molecular yardstick against which native fishes and their ecologies can be gauged. An inability to apply these metrics will diminish historical legacy (i.e. species and ESUs) as well as contemporary adaptation (i.e. MUs). Conflicts will emerge as basin-level biodiversity is prioritized against an anthropogenic future in which climate-induced dewatering juxtaposes with non-sustainable water use in a Cadillac Desert (Sabo *et al.* 2010b).

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This study stems from 20+ years of research by M.R.D. and M. E.D. on the evolution, ecology and conservation of freshwater fishes in the arid lands of western North America. The microsatellite data are one aspect of M.W.H.'s Master's Thesis. We interact with closely with applied conservation practitioners to ensure that our broad, multidisciplinary research reflects the best science available and that our management recommendations are adaptive, relevant, and sustainable.

Data accessibility

DNA sequences: GenBank accessions JX871896–871938.
 Individual microsatellite and haplotype data: DRYAD
 entry doi:10.5061/dryad.h16ss.

Appendix I

Summary of 16 microsatellite DNA loci used to genotype 1092 Bluehead Sucker (*Catostomus discobolus*). Listed are Locus = name; Motif = Di (two nucleotides), Tetra (four nucleotides); A = number of alleles; Range = allele size in base pairs (bp); H_E = expected heterozygosity across all populations. Loci are described in Tranah *et al.* (2001).

Locus	Motif	A	Range (bp)	H_E
Dlu27	Di	25	187–261	0.66
Dlu209	Di	41	132–248	0.67
Dlu229	Di	26	120–180	0.56
Dlu230	Di	28	100–176	0.60

Appendix 1 Continued

Locus	Motif	A	Range (bp)	H_E
Dlu233	Di	17	117–191	0.69
Dlu245	Di	10	185–229	0.51
Dlu257	Di	57	147–515	0.81
Dlu276	Di	27	109–175	0.68
Dlu409	Tetra	30	144–258	0.89
Dlu434	Tetra	28	178–310	0.73
Dlu456	Tetra	40	142–310	0.87
Dlu482	Tetra	28	140–280	0.83
Dlu4153	Tetra	42	167–335	0.90
Dlu4184	Tetra	31	154–282	0.86
Dlu4235	Tetra	53	171–463	0.88
Dlu4300	Tetra	39	186–338	0.91