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Wild, Native, or Pure: Trout as Genetic Bodies

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Abstract

Advances in genetics and genomics have raised new questions in trout restoration and management, specifically about species identity and purity, which fish to value, and where these fish belong. This paper examines how this molecular turn in fisheries management is influencing wild and native trout policy in Colorado. Examples from two small Colorado watersheds, Bear Creek and Sand Creek, illustrate how framing trout as genetic bodies can guide managers to care for or kill trout populations in the interest of rectifying decades of genetic disruption caused by human activity. While trout management has typically relied on human intervention, the turn to genetic science is prompting new classifications of lineage and taxa, altering long-standing conservation priorities, and reorienting the manipulation of biological processes such as reproduction and dispersal. As a result, other social and ecological factors may be pushed to the margins of management decisions. These changes warrant greater conversation about the consequences of molecular analyses and the values embedded in trout science and conservation more broadly.

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The Wrong Fish

In 2012, analyses of DNA revealed a surprising secret about Colorado's state fish, the greenback cutthroat trout (*Oncorhynchus clarkii stomias*). The organism believed to be the greenback cutthroat trout, which for more than forty years had been the focus of state and federal recovery efforts in Colorado streams and lakes, was, in essence, the wrong fish. Populations of greenback cutthroat trout that had been carefully reared, protected, and restored to Front Range habitats were more likely variants of a different subspecies, the Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*). The markings and geographic range of the fish had seemed to distinguish it from other Colorado River cutthroats (Behnke 1979), but by the 1990s, identifications by phenotype (e.g., morphology and meristics) and watershed were gradually being replaced by genetic tests that could distinguish differences in organisms invisible to the human eye or geography (S. J. O'Brien and Mayr 1991; Rogers 2010). The same DNA analyses that had revealed the restored populations as the "wrong" fish also discovered one remaining population of greenback cutthroat that matched museum specimens used for historical reference.[1] These pure greenback cutthroats were finning obscurely in Bear Creek, a small tributary of the Arkansas River on the flanks of Pikes Peak (Metcalf et al. 2012).

The discovery that decades of greenback cutthroat trout recovery had been based on a case of mistaken identity proved disorienting to the scientists, wildlife officials, and anglers who had been studying, managing, or catching these fish for years. In little more than a decade, the observation-based biology that had long guided fisheries management faced challenges by laboratory tests that could ascertain tiny differences in the lineage and genetic composition of trout and other organisms (see Bestgen, Rogers, and Granger [2019] for a comparison of approaches). As a result, the scientific understanding of cutthroat trout has been effectively reconstructed from one based in direct experiences with fish in particular places to more abstracted DNA analyses of fish tissue or environmental samples (e.g., Tautz et al. 2003; Blaxter 2004; Metcalf et al. 2007, 2012).

The advent of better, cheaper, and faster molecular techniques has brought trout genetics into sharper focus, making the fish legible and governable as *genetic bodies*. Genetic and genomic analyses have raised new questions in trout restoration and management, specifically regarding species purity, which fish to value, and where these fish belong. Many of these questions are now routinely addressed at the molecular scale (Allendorf et al. 2004; Rogers 2012; Rogers et al. 2018). As these issues of lineage and purity come to the forefront of management decisions, genetic science is increasingly called upon to help decide the fate of fish across entire watersheds.

In this paper, we examine the changing science and management of Colorado's cutthroat trout populations. We consider the ways this molecular turn is influencing wild and native trout policy, and how science, technology, and values shape what are often life or death decisions about trout stocks and their composition. We argue that the shift to thinking about trout—and, by extension, other organisms—as genetic bodies is ushering in an era where management decisions are reduced to questions of technology and purity rather than accounting for more diverse priorities of ecology, culture, ethics, economics, long-standing relationships between fish and people or integrated forms of scientific knowledge. While trout management has typically relied on human intervention, the turn to genetic science is bringing new lineages and taxa into being, altering long-standing conservation priorities and intensifying the manipulation of biological processes such as reproduction and dispersal. As a result, other social and ecological factors are pushed to the margins of management decisions. These changes, we argue, warrant greater conversation about the consequences of molecular analyses and the values embedded in trout science and conservation more broadly.

Cutthroat trout are just one of many organisms today for whom managers are making life and death decisions based on subtle differences in genetic makeup or genealogy. Molecular scale analyses now guide wildlife officials in determining the fate of an array of organisms ranging from wolves and bison to the western toad (e.g., Goebel et al. 2009). For trout, managers frequently target hybridized or nonnative populations with toxicants and replace them with fish deemed native to a given watershed. While the use of fish toxicants for management is not new, molecular analyses are contributing to shifting geographies of eradication and conservation. Streams or populations that were once in situ conservation priorities may now be targeted for treatment with toxicants (and vice versa).

In the following, we discuss how molecular analyses are producing new understandings of trout. We examine the case of cutthroat trout in Colorado, focusing on how the state of knowledge evolved from the end of the twentieth century, prior to widespread genetic analysis of trout populations, to today. Phylogenetic analyses of mitochondrial DNA have been used to gain greater precision and clarity in trout identification and in the process have profoundly challenged assumptions about cutthroat trout diversity and distribution. We then explore how genetic information has been mobilized in recovery efforts for two cutthroat trout subspecies, the greenback and Rio Grande (*Oncorhynchus clarkii virginalis*). Through these cases, we consider the life and death consequences of new genetic knowledge for the affected individuals and populations. Molecular analyses authorize acts of care or killing by state and federal agencies, but genetic information can also open up or challenge agency priorities and management plans. In addition, privileging management goals of purity and nativeness can lead to new questions and challenges, including the creation of vulnerable populations that require repeated interventions to ensure their survival.

Trout as Genetic Bodies

The use of molecular techniques has made trout newly *legible* as genetic bodies. Legibility here refers to the ability to unambiguously identify, classify, and manage places, people, organisms, or property (see Scott 1998). By introducing greater precision and standardization to fish identification, and thereby clarifying murky evolutionary lineages, molecular techniques have expanded and deepened the scientific management of organisms like trout. Where previously trout were identified by phenotype and watershed, they are now subject to analyses that identify and classify organisms based on seemingly objective metrics associated with DNA sequencing. The interplay between conservation and science has brought trout into focus as genetic bodies, but these newly genetic bodies also present challenges for conservation.

Key among new molecular tools and techniques are mitochondrial DNA and environmental DNA. Because the genetic information encoded in the mitochondria of animals evolves relatively quickly and is less complex than nuclear DNA, mitochondrial DNA analysis has become increasingly common in ecology and evolutionary biology. By identifying similarities in mitochondrial DNA sequences that indicate shared ancestry, researchers can reconstruct phylogenetic trees depicting evolutionary relationships between different trout populations. More recently, fisheries scientists and managers have added environmental DNA to their molecular toolboxes. Environmental DNA is genetic material found in water, sediment, or air samples rather than directly extracted from its biological source (Thomsen and Willerslev 2015). Aquatic scientists can now analyze environmental DNA to detect nonnative, hybrid, or genetically impure fish from simple water samples, without ever encountering the organism as a whole.

The proliferation of molecular data and the ability to reconstruct phylogenetic relationships based on these data have led to a paradigm shift in how species are understood and delineated. The concept of species has long presented a challenge for biologists, with debate around both the ontological basis of species and the epistemological problem of establishing criteria to distinguish species from one another (de Queiroz 1998; Freudenstein et al. 2017). Over the past few decades, the evolutionary and lineage concepts of species, which view species as single lines of descent represented on phylogenetic trees, have gained favor over the biological species concept, which conceptualizes species as groups of interbreeding populations reproductively isolated from other groups (Mayr 1942). This paradigm shift has significant implications for the science and management of trout as we expand on in later sections.

For most wildlife managers, the goal of using new molecular tools and genetic information is to improve the conservation of biodiversity, especially of native or threatened taxa (e.g., US Forest Service 2018; Swanson 2019). Across the US Rocky Mountain West, genetic and genomic studies have identified introgressive hybridization as a critical threat to native wild trout (Boyer, Muhlfeld, and Allendorf 2008; Metcalf, Siegle, and Martin 2008). For some, such as the westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), genomic extinction due to hybridization with nonnative rainbow trout (*Oncorhynchus mykiss*) is widely recognized as one of the greatest threats to the species' survival (Allendorf et al. 2004; Schwartz, Luikart, and Waples 2006). DNA analyses have found that many of western North America's "native" trout are, in fact, genetic hybrids (Allendorf and Leary 1988; Allendorf et al. 2001; Rubidge, Corbett, and Taylor 2001; Metcalf, Siegle, and Martin 2008; McKelvey et al. 2016). Restoration and rewilding projects that aim to combat or repair hybridization have subsequently been undertaken by state and federal wildlife agencies and tribal fish commissions (e.g., Boyer, Muhlfeld, and Allendorf 2008; Simpson and Haggard 2020). Put broadly, new molecular tools have legitimized concepts of nativeness, belonging, and genetic purity as quantifiable management objectives that in the interest of conserving biodiversity may compel action. The ability to evaluate the purity of an organism now spurs recommendations on how to manage and restore trout populations: even a trace of genetic mixing may be disqualifying (Allendorf et al. 2004).

Wild, Native, or Indigenized

As issues of lineage and genetic composition are brought into sharper focus, certain complexities of ecology, history, and management are necessarily simplified or overlooked. The molecular turn has shifted questions about where trout belong to be addressed increasingly as a matter of DNA, which is used as an authoritative signal for nativeness and belonging.[2] In other words, the shift toward thinking of trout as genetic bodies narrows the field of vision, focusing management on questions of technology and purity rather than engaging more diverse ecological, economic, or cultural considerations.

In Colorado, recent findings about native cutthroat trout lineages and genetics have brought to the fore practical and philosophical questions about how DNA analyses will guide management. Categorizations of wildness, nativeness, and purity are complicated not only by changing assumptions about trout taxonomy and genetics, but also by the history of anthropogenic fish transfers and recent decades of attachment by anglers to particular fisheries. "Wild trout," which exists as a formal designation in Colorado and many other states, signifies that a population is self-sustaining and not dependent upon stocking operations for its sustenance (J. C. Brown 2015; Colorado Wildlife Commission 2008). The longer a population remains in a watershed successfully reproducing, the wilder, in a sense, that population becomes. "Native trout," meanwhile, describes the origins of a fish population or lineage: by most accounts, if a particular species (or subspecies/lineage) exists in a watershed without human intervention, then it qualifies as native (D. Brown 2016; Burgert 2019). Native trout have traditionally been assumed to fit within watershed boundaries, with Colorado River cutthroat trout occupying the Colorado River basin, the Rio Grande cutthroat trout inhabiting the Rio Grande watershed, and so on.

Wildness in the context of trout populations sounds like a relatively simple matter to evaluate: are the fish reproducing and sustaining themselves generation after generation?[3] The deeper historical origins of nativeness, however, prove more problematic to identify for many trout populations, and in some contexts what "belongs" biologically or culturally is not so clear (Helmreich 2005; Trigger 2008; D. Brown 2016). This is especially true in settler colonial environments, where efforts to restore "native" species may be interpreted as decolonizing the landscape by some and as fostering xenophobia by others (W. O'Brien 2006; Mastnak, Elyachar, and Boellstorff 2014). Species can also be reconceptualized over time in ways that reassign such fundamental attributes as nativeness. The concept of "emergent autochthony," for example, recognizes that nonnative species can become effectively indigenized, achieving a place of belonging culturally or ecologically (Helmreich 2005; Trigger 2008; Trigger et al. 2008; Blair 2017). Insights from traditional ecological knowledge and indigenous cultures also often challenge dualistic constructions of native or non-native, pressing instead for an emphasis on relationships, which can vary widely even within a single location (Whyte 2013; Todd 2014, 2017; Kimmerer 2015; Hoogeveen 2016).

All of these ideas point to the need to broaden existing conversations around nativeness, purity, and environmental "belonging" in trout management. The open-endedness or complexity of these perspectives presents challenges to policy prescriptions, however, where in recent decades managers have leaned increasingly on genetic analyses for the final word. We now turn to the biogeography of the cutthroat trout, considering how molecular analyses have reshaped scientific ideas about which trout belong where.

A Murky Biogeography

The biogeography of cutthroat trout in western North America has long been clouded with uncertainty. Even to lifelong scholars of trout taxonomy, the difficulty of distinguishing one species or subspecies from the next has proved vexing as coloration, patterns of dark spots, morphology, and numbers of scales often failed to be clearly diagnostic. Even the seemingly stable criterion of geography—with divergent fish species or subspecies separated by watershed divides—was largely rendered moot by widespread stocking and the often-unregulated translocation of fish (Dowling and Childs 1992; Perry, Lodge, and Feder 2002; Boyer, Muhlfeld, and Allendorf 2008). Since the late 1800s, the distribution of cutthroat trout populations reflected not just geographic barriers and watershed boundaries but also regular occurrences of "bucket biology": people moved fish from one place to another without fully understanding which fish they were handling, where those fish originated, or how the fish would interact with other organisms once they arrived. Cutthroat trout proved relatively easy to transport and cultivate, and also hybridized readily between subspecies and with rainbow trout, which were widely stocked beyond their native range throughout the late nineteenth and twentieth centuries (Halverson 2010).

By the mid-twentieth century, most cutthroat trout subspecies were found only in small portions of their presettlement ranges, due to a combination of habitat loss, fragmentation, and hybridization and competition with introduced trout (Smith 1984). The decline of the greenback cutthroat trout was particularly dramatic. By 1919, there were no known extant populations in the South Platte River watershed, although a handful of small isolated populations were reported in tributaries of the upper Arkansas River (Young and Harig 2001). Less than two decades later, by 1937, the greenback cutthroat was presumed extinct.

In 1968, however, the state's preeminent fish biologist, Dr. Robert Behnke, identified what he believed to be an isolated surviving population of greenback cutthroat trout in the South Platte River basin. The discovery led to the fish gaining early protection under the US Endangered Species Act (ESA; Wang and White 1994; Fendt 2019). The US Fish and Wildlife Service (US FWS) developed the first recovery plan for the species in 1978 (the plan was modified in 1998). Recovery goals included the establishment of twenty stable populations occupying at least fifty hectares of lakes or ponds and fifty kilometers of stream. At least five of the populations needed to be in the Arkansas River watershed, with the remainder occupying South Platte River tributaries (US FWS 1998). By the late 1990s, there were eighteen stable populations in the South Platte and three in the Arkansas River watershed (Young and Harig 2001).

At that point, prior to molecular analysis, it was believed that the greenback cutthroat was one of fourteen subspecies of North American cutthroat trout (two of which were presumed to be extinct: the yellowfin cutthroat trout [*Oncorhynchus clarkii macdonaldi*] and the Alvord cutthroat trout [*Oncorhynchus clarkii alvordensis*]). The common understanding, based on Behnke (1979, 1992), was that cutthroat trout had diverged from rainbow trout somewhere between 2 and 6 million years ago and established themselves as the exclusive native trout species of the United States' interior West.[4] Cutthroat trout then gradually diversified into subspecies or lineages separated by watershed boundaries. Prior to molecular studies, four cutthroat subspecies were considered native to Colorado: the greenback, Colorado River, Rio Grande, and yellowfin (US FWS 1998; Young and Harig 2001; Metcalf et al. 2007).[5] This classification scheme represented the consensus among fisheries scientists until DNA sequence-based methods and fossil evidence began to raise doubts in the 1990s and 2000s. By the mid-2010s, several new classification schemes had been proposed (e.g., Loxterman and Keeley 2012; Wilson and Turner 2009), and in 2015 the Western Division of the American Fisheries Society convened a meeting of experts to reevaluate cutthroat trout phylogeny and classification. The majority of panelists agreed that molecular studies (coupled with meristics and geological history) supported the existence of twenty-five subspecies rather than the fourteen identified by Behnke (Trotter et al. 2015), but even in the wake of DNA studies, there was a recognized lack of consensus on the evolutionary relationships among subspecies, the role of nonmolecular data in taxonomic decisions, and even the utility and meaning of the "subspecies" category. Alluding to the greenback cutthroat trout recovery program, scientists at the 2015 workshop recognized that this "erosion of consensus . . . has already disrupted the recovery program for one ESA-listed subspecies and could affect recovery programs for others" (Trotter et al. 2015, 10).

Fish Out of Time, Fish Out of Place

In the early 2000s, just as the greenback cutthroat trout was poised for delisting under the ESA, a few scientists started raising concerns about the robustness of greenback recovery in Colorado (Young and Harig 2001). Critiques of the plan suggested that the subspecies' distribution, lineage, and life history remained poorly understood and that the quantitative criteria for recovery lacked biological justification. For example, abundance thresholds were deemed inadequate for long-term persistence of greenback populations, habitat requirements favored recovery in lakes over streams, and restoration sites were often small, isolated habitats in headwater streams or high-elevation lakes that were not part of the trout's presumed historical range (Young and Harig 2001). This isolation might protect populations from the effects of nonnative species invasion but would also block gene flow and prevent fish from developing their characteristically mobile life histories.

As critiques mounted, the uncertainty of Colorado's cutthroat trout distribution started to attract the attention of research scientists and fisheries managers. New DNA sequence comparisons of mitochondrial gene segments threw into question some of the fundamental assumptions about the distribution and identity of cutthroat trout in Colorado. Phylogenetic analysis of molecular markers in populations previously identified phenotypically as pure greenback cutthroat trout yielded "an unexpected and complicated distribution of genotypes" with "divergent evolutionary lineages [that] did not separate geographically on either side of the Continental Divide" (Metcalf et al. 2007, 4448). In other words, when analyzed by genotype, most of the supposedly pure greenback cutthroat populations east of the Continental Divide shared a lineage with Colorado River cutthroat trout from the west side of the Continental Divide. As Metcalf et al. (2007) pointedly wrote, "Our results imply that more than two decades of work towards bringing the species back from extinction have failed to improve the species' status" (p. 4446).

Before phylogenetic analyses could introduce a new level of precision and clarity to cutthroat trout management, they first presented a series of inconvenient truths that challenged state and federal recovery efforts. The initial tests of Colorado trout genetics so profoundly challenged existing assumptions about how cutthroat subspecies were distributed across watersheds and the major east–west barrier of the Continental Divide that one state fisheries scientist surmised greenback cutthroat trout might be native to *western* slope watersheds and linked more closely than had been previously realized to Colorado River cutthroat trout (see Metcalf et al. 2007; Rogers 2010).

Only when scientists were able to compare contemporary DNA of extant cutthroat trout populations with DNA from a handful of nineteenth-century museum specimens—gathered before widespread trout relocations ramped up in the 1880s—did decades of assumptions about trout distribution and diversity fully unravel. A 2012 article in *Molecular Ecology* reported the main findings of this study (Metcalf et al. 2012). First, where previous studies had identified four subspecies of cutthroat trout in Colorado, phylogenetic analyses of museum specimens identified six divergent lineages (see Figure 1 for presumptive native ranges of Colorado's native trout, pre- and post-genetic analysis). The Colorado River cutthroat was found to have two separate lineages, referred to as "green" and "blue," with versions of the green lineage found, somehow, on both sides of the Continental Divide. In addition, a sixth subspecies was documented, the San Juan cutthroat trout, which was thought to be extinct, until 2018 when populations matching its historic DNA were found surviving in small headwater streams in southwestern Colorado ("Colorado Parks and Wildlife" 2018).

Second, this set of phylogenetic analyses finally dispatched any remaining confidence in the historic understanding of greenback cutthroat identification and distribution, specifically: "Importantly, we discovered that the cutthroat lineage historically native to the South Platte, that at one time was declared extinct, *persists in a single stream outside its native range*" (Metcalf et al. 2012, 9, emphasis added). That single stream was an inconspicuous drainage, Bear Creek, located high on the southeast slopes of Pikes Peak, in the upper reaches of the *Arkansas River* watershed. However, the new analyses also highlighted that the true native cutthroat trout of the Arkansas River watershed was likely not the greenback, but rather the extinct yellowfin cutthroat. In short, Bear Creek—outside of the historical range of the greenback cutthroat—was found to be home to the only

Figure 1. Native ranges of Colorado's native cutthroat troutlineages, before (left) and after (right) genetic analysis (credit: Colorado Parks and Wildlife).

documented population of genetically pure greenback cutthroat trout in the state, at least as defined by phylogenetic analysis of museum specimens from the South Platte drainage.

This discovery marked a key step in the molecular turn in trout science and management by underscoring that earlier attempts to manage Colorado's cutthroat trout were inherently flawed due to the inability of observation-based biology to grasp the complex realities of trout as genetic bodies. The confusion during the previous decade about trout lineages was based not in a wider-than-expected distribution of greenback cutthroat trout, as initially suspected, or a closer-than-realized ancestral link to Colorado River cutthroats, but in the fact that nearly *all* the fish tested from remote drainages across the state turned out to be offspring or hybrids of Colorado River cutthroat trout. The lone population of actual greenback cutthroat trout had been so obscure it had long been assumed to be unimportant or simply "weird" (Rogers 2012). It was also surviving, generation after generation, in the "wrong" watershed. In effect, the greenback had become both a fish out of time and a fish out of place, thanks to human activities spanning more than a century and new understandings produced by phylogenetic analysis.

In the sections that follow, we examine how this new focus on trout as genetic bodies representative of identifiable evolutionary lineages has impacted management, with life and death consequences for the individuals and populations being analyzed.

Managing New Geographies of Trout

As scientists find themselves increasingly able to evaluate species' identity and distribution through tests conducted at the molecular scale, fisheries managers face questions about what to do with these new insights. This poses broad questions of policy: for example, how should ESA protections be engaged to respond to new cutthroat trout taxonomies and revised notions of population size and location? It also raises questions about what to do with trout for whom wildness and nativeness are especially fraught, for example, those that are found outside of their presumed native range, those that are genetic hybrids, and those that are the result of previous rounds of restoration.

Despite these complications, state and federal management agencies now routinely use genetic insights and tools to guide what are often life or death decisions about trout populations. Phylogenetic analyses have led to the reevaluation of greenback cutthroat trout in Bear Creek from mere oddities to prized genetic stock, subject to intensive protection, reproduction, and reintroduction efforts. For other populations, the results of genetic tests diminish their value due to concerns about hybridization. For example, 150 kilometers south of Bear Creek, genetic analyses indicating hybridization led managers to target wild cutthroat trout in the Sand Creek Lakes for eradication, clearing the watershed to install genetically pure Rio Grande cutthroat. Examples from these two Colorado watersheds, Bear Creek and Sand Creek, illustrate how framing trout as genetic bodies can compel managers to care for or kill trout populations in the interest of rectifying decades of genetic disruption caused by human activity.

The Right Fish: Bear Creek Greenback Cutthroat Trout

Following the molecular analyses that identified a lone population of greenback cutthroat trout in the "wrong" watershed (Metcalf et al. 2012), scientists and managers have grappled with questions about what constitutes greenback recovery, how to manage the populations previously believed to be greenbacks, and how to weigh genetic purity versus long-term viability of the subspecies.

If recent genetic tests are correct in identifying the greenback as the true native trout of the South Platte River watershed, and if the yellowfin cutthroat was the former native trout of the Arkansas River watershed, then the sole wild greenback population in Bear Creek is not *native* to the stream where it has managed to survive for well over a century. Instead, the Bear Creek fish were almost certainly introduced in the upper watershed by a single individual, J. C. Jones, who in the 1870s brought trout fishing to a hotel enterprise he was developing near Pikes Peak (Rogers 2012). A strict application of native trout ideals would argue that these Bear Creek greenback cutthroats should be removed and restored to the South Platte River basin, but that would cut directly against management goals that prioritize *wild* trout. After all, the Bear Creek trout have successfully persisted through the decades while being largely ignored by land managers and recreationists.[6]

Despite the realization that greenback cutthroats are not likely native to the watershed, Bear Creek's trout have not been slated for eradication but have instead been protected in situ and subject to intensive efforts to preserve and propagate the subspecies *ex situ*. Starting with just 65 fish, managers at federal and state fish hatcheries in Colorado have now raised thousands of Bear Creek trout offspring for recovery efforts (Finley 2014). The very factors that led to the preservation of this genetically pure population, however, also threaten its viability. The source population of greenback cutthroat trout in Bear Creek is small, with approximately 800 fish occupying a short, hydrologically isolated stretch of headwater stream. The population likely experienced genetic bottlenecks during more than a century of isolation, and progeny raised for recovery and restocking in hatcheries have shown alarming rates of genetic defect and limited viability (US FWS 2014; Fendt 2019).[7] As a result, scientists are intensively managing their reproduction using a technique called gene matrixing, which relies on an algorithm to match least closely related fish to improve viability and survival.

Hatchery-raised progeny of Bear Creek greenback cutthroat trout have now been stocked in several isolated streams, lakes, and reservoirs in the South Platte watershed, in some cases replacing populations that had been restored during earlier rounds of greenback recovery efforts. To prevent genetically pure Bear Creek greenback cutthroat trout from hybridizing, any existing fish in these locations are first removed. For example, West Creek in Rocky Mountain National Park was a site of previous (misidentified) greenback cutthroat trout restoration (US FWS 1998). Managers now face a dilemma about if and how to value such populations. Relabeled as green lineage Colorado River cutthroat trout, West Creek's fish have been removed via nonlethal electrofishing and relocated (Fendt 2019). Hybridized or nonnative fish in other locations have simply been eradicated with toxicants. In some places, new barriers to fish passage must also be constructed to protect transplants from mixing with other trout (e.g., Paul 2018).

The most ambitious of the Bear Creek greenback cutthroat trout restoration efforts will take up to two decades, cost nearly $2 million, and create thirty-seven miles of interconnected waters in the upper Cache la Poudre drainage (a tributary to the South Platte), which as a whole must be kept *disconnected* from waters downstream (Colorado Trout Unlimited 2020). Long-term, the success of this effort to establish a pure, native, and (eventually) wild greenback cutthroat trout population rests upon significant modifications to high-elevation catchments, repeated interventions to ensure species purity at the molecular level, and survival and reproduction by individuals. In this respect, the largest native trout recovery effort in Colorado, a project that aims to naturalize and rewild the state fish in pure form, will be produced through a series of carefully orchestrated human manipulations. A similar push for species purity is underway farther south in Colorado, where the Sand Creek watershed is a focus of Rio Grande cutthroat management.

"Poison out the Mongrels": Managing Rio Grande Cutthroat Trout

Part of Great Sand Dunes National Park and Preserve, Upper and Lower Sand Creek Lakes sit in picturesque cirques high in the Sangre de Cristo

Mountains of southern Colorado. For visitors who navigate the bumpy dirt access road and hike seven kilometers into the upper Sand Creek basin, the lakes have long offered stunning views, relative solitude, and waters teeming with large cutthroat trout.

The Sand Creek drainage is not connected by surface flow to the broader Rio Grande basin and was considered fishless prior to stocking (McGee, Todd, and Terry 2019). The Colorado Division of Wildlife (CDOW, now Colorado Parks & Wildlife) first brought fish into the Sand Creek Lakes in 1974. The agency introduced novel hybrids of Colorado River and Yellowstone cutthroat trout that CDOW called, seemingly without irony, the "Pikes Peak Native" (McGee, Todd, and Terry 2019). Agency officials were uncertain about trout survival and overwintering at the lakes, so they restocked them frequently over the ensuing years. Beginning in 1998, the agency shifted strategies and stocked the lakes with Rio Grande cutthroat trout, hoping to expand the occupied range for the pure strain of the subspecies. The Sand Creek watershed made an attractive recovery target with its isolated, clean, cold water bodies that were protected in a Wilderness area within a national park unit.

In 2019, federal officials published a study that detailed genetic assays of cutthroat trout sampled in Sand Creek lakes and streams. These described a genetic composition that demonstrated varying degrees of hybridization. During more than four decades of stocking, the fish in the two Sand Creek lakes had hybridized to include a mix of Yellowstone, Colorado River, and Rio Grande cutthroat trout, with a few rainbow trout genes sprinkled in (Figure 2) (McGee, Todd, and Terry 2019). In some cases, scientists were unable to see differences in the markings of fish that genetic tests proved to be rather different in origin: a 100 percent pure Rio Grande cutthroat, for example, looked nearly the same as a Rio Grande-Yellowstone-rainbow trout hybrid (McGee, Todd, and Terry 2019, 22). Most anglers who visited the lakes knew little about the ancestry or purity of the fish they were catching, referring to cutthroat trout they caught simply as *native* (and, for all but those few who knew about the stocking history, *wild* as well; personal communication 2007, 2019). They also knew that the fish in the lakes seemed to be thriving, with many of the trout reaching fifty centimeters or more in length.

Following the 2019 study, the National Park Service announced a plan to apply toxicants to remove all fish in the Sand Creek watershed's fish-bearing streams and lakes in order to restore a genetically pure native Rio Grande cutthroat population (Case 2019). Of course, Rio Grande cutthroat trout were only native to Sand Creek in a broad geographic sense, as the

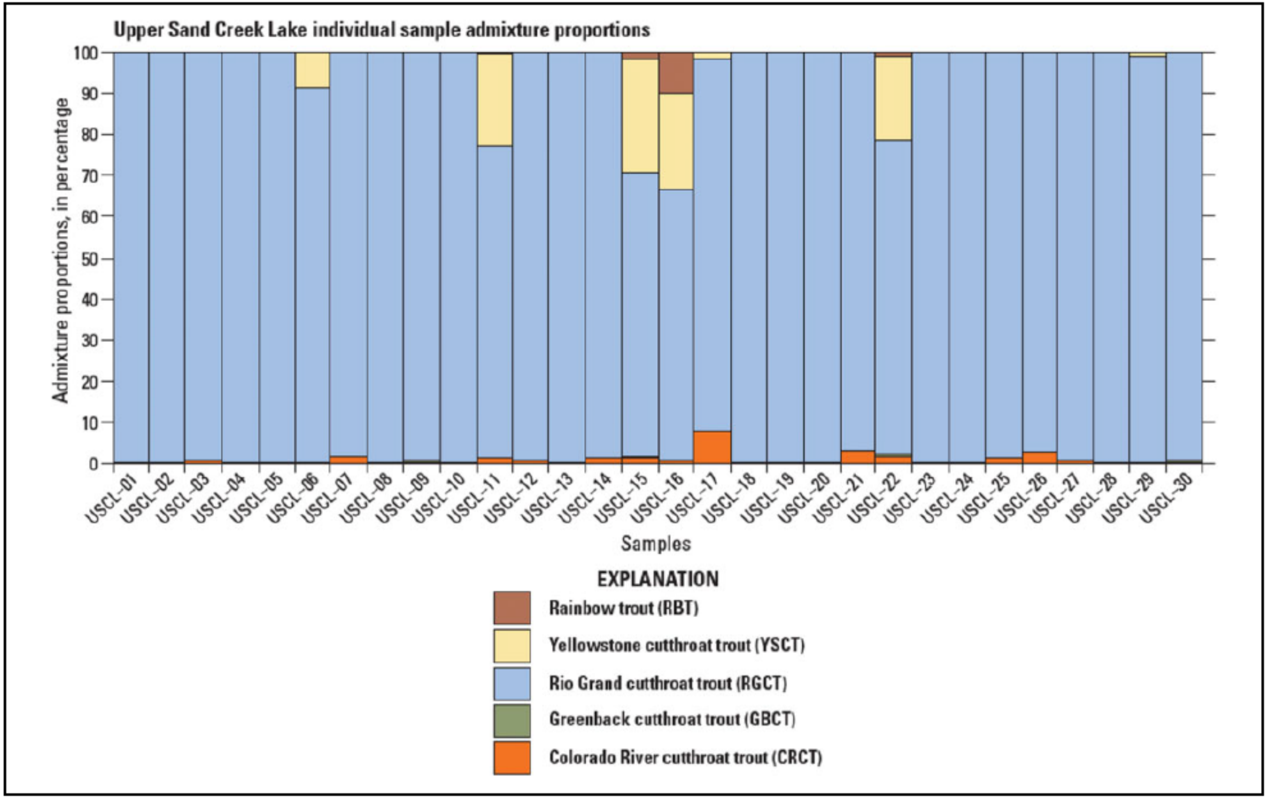

Figure 2. Genetic composition of trout in Upper Sand Creek Lake (from McGee et al. 2019, p. 22). Results of analyses from 30 fish samples using amplified fragment length polymorphism tests. Fish sample IDs are labelled across the x-axis. Note that "Greenback cutthroat trout (GBCT)" here refers to the earlier misclassified trout, which are now considered green lineage Colorado River cutthroats. "Colorado River cutthroat trout (CRCT)" refers to blue lineage fish.

drainage had no trout in it prior to human interventions. Sand Creek's hydrological isolation made it an ideal prospect for maintaining a protected genetic reserve for trout, though, as—stocking aside—most remaining pure cutthroat populations exist above hydrologic barriers such as waterfalls or constructed barriers such as dams or road culverts.

Although the Sand Creek cutthroat trout had a constituency of devotees in the anglers and backpackers who visited the lakes, concern about maintaining pure Rio Grande cutthroat reserves ruled the day and the watershed was treated with toxicants to eradicate all fish in September 2020 (Simpson and Haggard 2020). As one prominent trout writer tried to patiently explain to a reader who lamented the waste of killing off perfectly good trout in a similar case:

> It would be great if it were possible to eliminate all the alien and mongrel fish and at the same time use them, but it is not. The only way to save native fish from genetic introgression, competition and predation (and resultant extirpation or extinction) is to poison out the mongrels and aliens with rotenone. (Williams 2019)

The Abstract Trout

The Bear Creek and Sand Creek cases bring into view at least three important issues associated with understanding trout as genetic bodies. First, information provided by genetic tests prevailed upon wildlife officials and effectively motivated them to move beyond their own (or others') direct experiences with trout populations to take action based on laboratory-generated data. This is perhaps especially notable insofar as the lived encounters with trout in the Sand Creek basin had long been characterized as *wild experiences*: any self-sustaining populations of trout warranted a label as wild trout; visitors to the basin had to travel via foot or horseback into a remote and rugged backcountry to reach the lakes; and the character of the place itself very much met the terms of the Wilderness Act of 1964, as "an area . . . [with] outstanding opportunities for solitude or a primitive and unconfined type of recreation . . . " The upper Sand Creek watershed might seem distant from reductionistic scientific authority, but a molecular approach to management clearly has taken precedence here against alternative approaches that might, for example, attend more fully to relationships or assemblages, the sentience of individual organisms, or positioning animals as subjects (Hoogeveen 2016; Miller 2018; Fraser-Celin and Hovorka 2019; Satizábal and Dressler 2019; Gibbs 2020).

Second, in both cases, nativeness is a fungible concept. State and federal agencies have eradicated existing fish and will stock Rio Grande cutthroat trout in the Sand Creek watershed in order to "restore native plant and animal species" and "reclaim Great Sand Dunes National Park and Preserve for native *Oncorhynchus clarkii virginalis* (Rio Grande cutthroat trout)" (McGee, Todd, and Terry 2019, iii), despite the fact that trout did not exist in the basin until fisheries managers deposited them there. By most ecologists' definitions of the term, authentic restoration of the native plant and animal species in the Sand Creek watershed would mean returning it instead to a *fishless* condition. The same is true in upper Bear Creek, though none of the management scenarios for greenback cutthroat trout includes this as a possibility.[8] The ideal of managing a native fish population in these cases seems to serve other institutional or ecological interests, which may in their own right be well-founded, but requires co-opting the generally accepted meaning of *native*.

Third, the new genetic knowledge made available through mitochondrial DNA and environmental DNA testing comes with life or death consequences for the individuals and populations being analyzed. Tests demonstrating genetic purity now serve as critical managerial mandates, making these newly genetic bodies of trout increasingly subject to terminal restoration efforts. These require the eradication of some organisms—or, more accurately, entire populations—in order to bring forward genetically pure bodies. Molecular analyses reinforce control over fish populations, what Hoogeveen (2016) refers to as fish being "rendered technical," and help authorize acts of care or killing by state and federal agencies. At the same time, the proliferation of genetic data also serves to depoliticize these decisions, with managers pointing to the science as deterministic. As Williams argues above, "the only way to save native fish" becomes to eradicate nonnative and genetically impure bodies using toxicants, eliding any conversations about scientific uncertainty, lack of consensus, values, or the relational ethics that may be produced through human–fish interactions.

Some of the scientists interacting with and acting upon these new genetic insights remain unresolved about how fully to allow genetic tests to provide the final word, but these dissenters seem to recognize that they do so potentially at the peril of their scientific reputations. When a committee of experts gathered to discuss and analyze the changing understanding of native trout lineages in Colorado in 2014, they agreed to have their discussions published but only in a format where individuals would not be publicly identifiable and linked to particular views (US FWS 2014). When Robert Behnke, the Colorado trout scientist who had essentially defined the terms of the state's native trout knowledge for decades, was confronted with the results of genetic analyses of the fish he had studied, he lashed out against the authority of the genetic tests:

> Administrators and biologists making decisions based on genetic analysis lack an understanding of the various methods of modern molecular genetics, their limitations and how the data can be open to different interpretations. A little learning without an in-depth understanding of the subject matter can be dangerous .... Natural genetic variation once widespread in the ancestor that gave rise to the small, isolated populations was wrongly interpreted as evidence of hybridization .... If it looks like a duck, walks like a duck, and quacks like a duck, we should call it a duck. Getting into the molecular structure of a duck can result in confusion and chaos. Now substitute greenback cutthroat trout for duck, and move on (Behnke, as quoted in Williams, 2019).[9]

For other scientists, the response has been not to reject the insights gained through genetic tests, but to try to match these against long-standing efforts to identify trout lineages based on phenotype. The rekindled effort to pursue studies of meristics, spotting, and coloration to see whether these kinds of data could keep up with digital outputs of fish genomes brought its own set of conclusions: the genetic information appeared to be more reliable than observational data, but both approaches had merit in working through the complex geography and genealogy of native trout (Bestgen, Rogers, and Granger 2013, 2019; US FWS 2014).

Trout Science, Geography, and Values

The shifting understanding of trout science poses an array of questions to state and federal officials responsible for managing these fish. State fish and game departments that once concentrated their efforts on producing adequate supplies of trout for recreational anglers now face more nuanced choices about which fish they should value and which they should not. If the answer from an ecological or genealogical perspective conflicts with that provided by anglers or a well-established network of fish hatcheries, which actions then make sense to pursue?

In addition to these broad questions about how agencies should position their efforts, there are more particular questions of technology and science.

Since only short fragments of DNA from a handful of museum specimens are available to determine prestocking baselines of trout identity and distribution, how reliably or robustly can genetic tests establish the actual character of Colorado's native trout? For a population such as the Bear Creek greenback cutthroat whose genetic stock bottlenecked to a few hundred individuals during the twentieth century, to what degree should genetic purity be preserved or compromised in the interest of expanding its range and viability long-term?

This latter question is far from hypothetical. As we noted earlier, Bear Creek fish raised for recovery and restocking in hatcheries have shown alarming rates of genetic defect and limited viability (US FWS 2014; Fendt 2019). This has led some scientists to suggest intentionally crossing Bear Creek trout with Colorado River cutthroat or other trout to create a "recovery population" that is not genetically pure but might be more likely to survive over the long term across the South Platte River watershed (US FWS 2014; Fendt 2019). If we opt to protect genetically pure but fragile trout that require constant intervention to ensure their survival, what does that do, in turn, to goals of supporting wild, native fish?

Most of these questions remain unsettled, yet as next-generation genetic tests work to analyze organisms with ever-greater precision they seem likely to produce additional challenging questions. It is also important to recognize that the molecular turn in conservation reaches well beyond matters of trout and increasingly plays a role in management decisions more broadly (Hennessy 2015, 2020). As Allendorf, Hohenlohe, and Luikart (2010) point out, genetic analyses can be applied at scales ranging from the microbiome in a single individual to broad landscapes. Conservation efforts globally are mediated and promoted through digital technologies, big data, and other innovations that turn human decision-making into what appears to be data-driven, automated outcomes (Blair 2019; Perkins 2020).

The implications of this turn toward conservation genetics remain to be fully resolved, but genetic analyses are now increasingly framed as needing to "become a standard tool of conservation professionals" (Holderegger et al. 2019). The applications for conservation genetics appear to be vast (Allendorf, Hohenlohe, and Luikart 2010) and extend across diverse taxa, geographies, and political, ecological, or economic contexts. In other words, the questions we have raised here are by no means limited to cutthroat trout in Colorado. This case points to broader lessons about how evolving scientific practices and technologies reshape human relations with the biophysical world. In examining the turn toward understanding trout as genetic bodies, we take seriously the insights yielded by molecular approaches while also cautioning against an over-dependence on such approaches, which cannot provide easy answers to all ethical, sociocultural, and ecological concerns.

Colorado trout have been actively managed for decades, but with the turn to genetic science these fish may become even more intensively analyzed and manipulated at the molecular scale. As one fisheries scientist envisioned this effort, “Careful evaluation of hatchery stocks for genetic diversity and evidence of viability loss due to inbreeding is essential. It may be prudent to develop a brood stock management plan that stipulates mating designs, refreshment and retirement rates of brood stock, and steps to reduce domestication selection (e.g., supplying wild feed, and naturalized conditions in captivity)” (US FWS 2014). It remains to be seen how questions of wildness, nativeness, and purity will be resolved when it comes to the management or production of cutthroat trout in Colorado and elsewhere. In many cases, these three qualities may prove to be incompatible, building uncertainty into the question of which values will prevail upon these new forms of genetic bodies.

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Notes

1. The taxonomy of the Bear Creek trout has yet to be fully settled, but we refer to the fish as greenback cutthroat trout here following current common usage. Additional genetic tests may further rewrite the geography of Colorado trout.

2. Interestingly, this is occurring even as ecological and social scientists have critiqued the ambiguity and racialized meanings of labels such as native, alien, exotic, and invasive (Davis et al. 2011).
3. This is not to suggest that wildness, itself, is a simple concept (e.g., Snyder 1990; Cronon 1995; Lowe 2006) but rather that many fisheries managers view the term in a relatively limited way.
4. It is now believed that cutthroat trout may have diverged from rainbow trout much earlier, as fossil evidence indicates that cutthroat trout were present in the Lahontan Basin for 10.5 million years (Stearley and Smith 2016).
5. The yellowfin cutthroat trout was described and considered extinct dating back to the early 1900s (e.g., Behnke 1979). Its native range and relationship to other cutthroat subspecies remains uncertain, though many now consider the fish likely to be the native cutthroat to the Arkansas River watershed (Metcalf et al. 2012; Rogers 2012; Bestgen, Rogers, and Granger 2013).
6. The lack of attention might also be viewed as neglect: local residents, managers, and scientists were aware that the Bear Creek fish seemed different, but the watershed was better known for its popular motorcycle and mountain biking trails, many of which exacerbated fine sediment loads in the creek and potentially threatened trout spawning.
7. Interestingly, the fish appear to thrive in the wild in Bear Creek. The genetic liabilities only become evident in the hatchery-raised offspring (see US FWS 2014, 28).
8. We are not advocating for the eradication of fish in either basin, but a consistent application of ecological restoration principles would seem to point in this direction.
9. Behnke died in 2013 while many of the implications of the new genetic data were still unclear.

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