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Article

Does Habitat Restoration Increase Coexistence of Native Stream Fishes with Introduced Brown Trout: A Case Study on the Middle Provo River, Utah, USA

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Abstract: Restoration of altered or degraded habitats is often a key component in the conservation plan of native aquatic species, but introduced species may influence the response of the native community to restoration. Recent habitat restoration of the middle section of the Provo River in central Utah, USA, provided an opportunity to evaluate the effect of habitat restoration on the native fish community in a system with an introduced, dominant predator—brown trout (*Salmo trutta*). To determine the change in distribution of fish species and community composition, we surveyed 200 m of each of the four study reaches both before restoration (1998) and after restoration (2007 and 2009). Juveniles and adults of six native species increased in distribution after restoration. The variation in fish community structure among reaches was lower post-restoration than pre-restoration. Overall, restoration of complex habitat in the middle Provo River led to increased pattern of coexistence between native fishes and introduced brown trout, but restoration activities did not improve the status of the river's two rarest native fish species. Habitat restoration may only be completely successful in terms of restoring native communities when the abundance of invasive species can be kept at low levels.

Keywords: species-specific responses; habitat restoration; invasive species; brown trout

1. Introduction

Habitat restoration has become the dominant conservation activity in response to anthropogenic disturbance and degradation of streams and rivers, and is often a key component in the conservation plan of native aquatic species [1–3]. The immediate goal of most habitat restoration projects is to recreate the physical structure of the habitat that existed prior to anthropogenic alterations [4–6]. The underlying assumption is that native aquatic species will benefit from the restored habitat and their populations will increase such that, after some initial time period, the native community of aquatic organisms will re-establish. Under this assumption, success of habitat restoration projects is usually defined as an increase in species richness, ecological diversity, or population abundances. However, changes in these metrics may be determined by multiple factors that may or may not be related to the habitat restoration, and all species and communities may not respond in a similar way [7].

An additional factor that can impact native fish community structure in streams and rivers is introduced or invasive species. Invasive species can dramatically change native community structure through competitive and predatory interactions [8–12]. Simplification of stream habitats often favor generalist invasive species [3,8,13]. A corollary to this observation is that increasing the complexity of habitat structure through habitat restoration should lead to some degree of restoration of the native aquatic community resulting in some level of habitat-mediated coexistence of native and invasive species. The argument is that native species should be better adapted to natural conditions (*i.e.*, local adaptation) and that restoring habitat to a more natural condition should give native species an advantage in competitive or predator-prey interactions with non-native species. This is an attractive idea because it suggests that habitat restoration may ameliorate effects of invasive or introduced species that cannot be eradicated [13]. However, this hypothesis has seldom been tested in the context of stream restoration.

Recent habitat restoration of the middle section of the Provo River (between Jordanelle Reservoir and Deer Creek Reservoir) in central Utah, USA provided an opportunity to evaluate the effect of habitat restoration on the native fish community in a system with an introduced, dominant predator—brown trout (*Salmo trutta*). During the 1940's and 1950's, the river channel was straightened and levees were constructed for flood control with the exception of one segment about 1 km in length where the landowner would not allow the flood control work to be done [14]. In all other segments, channelization homogenized and simplified mesohabitats in the river channel. Brown trout were introduced to the river in the early 1900's and they quickly became a dominant species throughout the river [15]. Jordanelle Reservoir was constructed from 1987 to 1992 and provided downstream flood control thus eliminating the need for the downstream levees and channelization. Prior to construction of Jordanelle Reservoir, the river was unregulated and water diversion for agricultural irrigation sometimes resulted in low or no flows during the summer months in this middle section of the Provo River. As mitigation for dam construction and a trans-basin water transfer project (*i.e.*, the Central Utah Project), the levees along the middle section of the Provo River were removed, the river was restored to its formerly meandering channel, and side channels were constructed in an attempt to restore the river to a more natural condition. The assumption was that once restoration was complete, natural hydro-geomorphic processes would act to further develop and increase habitat complexity in and around this section of the river [14]. Additionally, there was a new water flow agreement that guaranteed a minimum base flow for this section of the river that was designed to maintain the fishery resources in the river. Habitat restoration activities on the middle section of the Provo River began in 1999 and concluded in 2008. Specific objectives of the restoration project included maintaining and enhancing the economically important brown trout fishery as well as improving and diversifying habitat for native fish species.

In this study we quantified response of the fish community to this habitat restoration effort. Our first objective was to determine if restoration of habitat structure favored native species expansion and increased coexistence of native fish species with the introduced brown trout. Our second objective was to determine if all species and age classes responded to habitat restoration in a similar way. To answer these questions we compared fish community structure and species-specific responses to pre- and post-restoration in the channelized reaches and compared the development of the subsequent fish community to that which was found in the reference reach, which had never been channelized.

2. Materials and Methods

2.1. Study Site

The Provo River watershed is located in Wasatch and Utah counties in central Utah, USA with a drainage area of 1743 km^2. The headwaters are located in the western end of the Uinta mountain range, the river drains to the west as it passes through the middle of the Wasatch mountain range, and empties into Utah Lake west of Provo, Utah, USA [16]. The focus of habitat restoration for this project was the middle Provo River, which is bounded by Jordanelle Reservoir on the north and Deer Creek Reservoir to the south. For the habitat restoration project, the river was divided into nine reaches of approximately equal length. The first reach was furthest downstream, beginning at the inflow to Deer

Creek reservoir and the ninth reach was the most upstream, beginning at the outflow of the Jordanelle Dam [14]. We used the same reach numbers designated in the restoration project to designate the four sample reaches for our study. Reach 4 was the un-channelized reference reach, and Reaches 3, 6, and 8 represented channelized sections that were restored as part of the Provo River Restoration Project (Figure 1). Restoration was completed in 1999 in Reach 8, 2003 in Reach 3, and 2005 in Reach 6. Pre- and post-restoration habitat measurements for some reaches are available in [17].

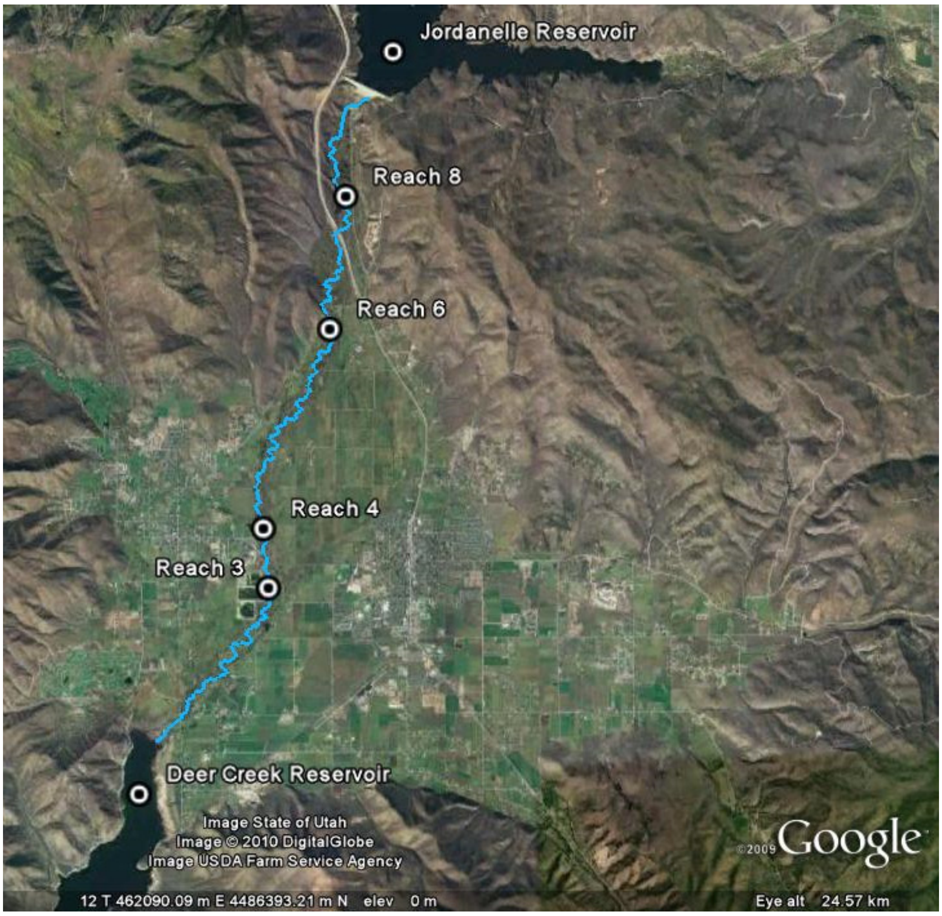

Figure 1. Aerial view of the study area. The Provo River is drawn in blue; it flows south–southwest. Study sites and reservoirs on the river are labeled. Map created in Google Earth® (https://www.google.com/earth/; Mountain View, CA, USA).

Native fish fauna of the Provo River mainstem includes nine species: Bonneville cutthroat trout (*Oncorhyncus clarki utah*), mountain whitefish (*Prosopium williamsoni*), Utah sucker (*Catostomus ardens*), mountain sucker (*Catostomus platyrhynchus*), redside shiner (*Richardsonius balteatus*), southern leatherside chub (*Lepidomeda aliciae*), speckled dace (*Rhinichthys osculus*), longnose dace (*Rhinichthys cataractae*), and mottled sculpin (*Cottus bairdi*) [18]. With the exception of Bonneville cutthroat trout, all of these species were found in at least one reach of the middle section of the Provo River just prior to the beginning of the restoration project. Two non-native species were found in this section of the Provo River as well—brown trout, and rainbow trout (*Oncorhynchus mykiss*).

Bonneville cutthroat trout were extirpated from the Provo River sometime after brown trout were introduced, and southern leatherside chub were found in low numbers and only in the reference reach (Reach 4) and Reach 3 near the mouth of a small creek (Spring Creek) [17]. To determine if habitat restoration would facilitate successful reintroduction of Bonneville cutthroat trout and southern leatherside chub, both species were reintroduced to the newly restored reaches during the project.

Southern leatherside chub (100 adults and 100 juveniles) were captured from Main Creek (a tributary of the Provo River that now drains into Deer Creek reservoir, and the only abundant source of southern leatherside chub in the Provo River drainage) near Wallsburg, Utah, USA, and moved in the same day to the newly constructed long side channel in Reach 8 in December of 1999 [17]. Bonneville cutthroat trout were stocked annually in the middle Provo River from 1997 through 2002. In total, several thousand individuals <200 mm total length were stocked over this interval [19].

2.2. Survey Methods

To determine the change in distribution of fish species and community composition, we surveyed 200 m of each of the four study reaches both before restoration (1998) and after restoration (2007 and 2009). Reaches 3, 4, and 8 were surveyed in 2007 and Reach 6 was surveyed in 2009. We used electrofishing methods (single pass) to survey study areas and document occurrence of species age classes. All fish were identified, counted, and assigned to an age-class group (juvenile or adult) based on length. We used the same size cutoffs between adult and juvenile as in Billman *et al.* [13]. Electrofishing methods in this relatively large system are quantitative for large-bodied fishes like salmonids only. For small-bodied species, the data are only reliable for indicating presence or absence. As with any survey method, there is always a possibility that rare species or size classes will not be found and thus recorded as missing, when in fact they are there at some low density. This problem of incomplete detectability may be especially concerning when species rich communities that contain many chronically rare species are compared. In the Provo River, all of the species compared are known to have occurred in relatively high densities when conditions were favorable (e.g., [13,18]). Our goal was to compare the established fish community before and after restoration. If we missed some small number of individuals of a given species during surveys, this would not really influence the conclusions of our study. Such small numbers of a given species would likely represent spatially or temporally transitory individuals, and not an established population. Hence, our estimate of the composition of the established fish assemblage is likely accurate.

2.3. Analysis

To determine changes in distribution we compared the number of reaches (of the four surveyed) occupied prior to restoration to the number occupied after restoration for each species age class. Both adult and juvenile brown trout and adult and juvenile mottled sculpin were found in all four study reaches prior to restoration. If native species expanded their distribution after restoration, this would suggest that habitat restoration provides greater opportunity for coexistence between native species and brown trout.

Evidence for increased coexistence is indicated in two ways by measures of similarity. First, post-restoration fish communities should converge relative to pre-restoration communities, and second restored reaches should converge with the reference reach. To determine if fish communities converged (*i.e.*, became more similar) after habitat restoration, we used ordination methods based on pair-wise similarity matrices of fish presence or absence. We generated similarity matrices based on the Bray-Curtis similarity index where pair-wise similarities are higher if samples are more similar and lower if samples are dissimilar [20]. To quantify similarity we estimated the multivariate dispersion among reaches for pre- and post-restoration fish communities [21,22]. Multivariate dispersion estimates the relative dispersion of groups in multivariate space such that a low value of multivariate dispersion indicates low variation in community structure among groups [22]. To visualize the relationship of fish communities among reaches through time (pre- and post-habitat restoration) we used non-metric multidimensional scaling (NMDS) [21,22]. We tested for differences among pre- and post-restoration fish communities using an analysis of similarity (ANOSIM) [21,22].

3. Results

The distribution of individual species and age classes changed from before to after restoration. Adult and juvenile brown trout and adult and juvenile mottled sculpin were found in all four study reaches both before and after restoration. Juveniles and adults of six native species increased in distribution after restoration. Juveniles and adults of rainbow trout decreased in distribution following restoration (Table 1). Overall, mean species/age class richness in restoration reaches increased from a mean of 4.33 (range 3–6) before restoration to 11.33 (range 8–15) after restoration. In the reference reach (Reach 4) species/age class richness increased from 9 to 14 over the same time period. Before restoration richness was clearly higher in the reference reach; however, after restoration richness in all reaches was higher and more similar. Reintroductions notwithstanding, neither southern leatherside chub nor Bonneville cutthroat trout expanded their distribution. Bonneville cutthroat trout were not observed in surveys before or after restoration and apparently failed to establish in the study area despite the stocking efforts. Adult southern leatherside chub were found only in Reach 4 prior to restoration, but after restoration adult and juvenile southern leatherside chub were found only in Reach 3 (in a location where they had been observed previously). Southern leatherside chub did not persist in Reach 8 where they were reintroduced in 1999.

Differences in similarity of fish communities pre- and post-restoration were significant (ANOSIM; $r = 0.667$; $p = 0.029$). Dissimilarity between pre- and post-restoration fish communities was determined by native fishes that were present in more reaches following restoration, and rainbow trout which were present in fewer reaches following restoration. The variation in fish community structure among reaches was lower post-restoration than pre-restoration (relative dispersion = 0.67 and 1.33, respectively). All restored reaches (Reaches 3, 6 and 8) were more similar to the reference reach after restoration (Figure 2).

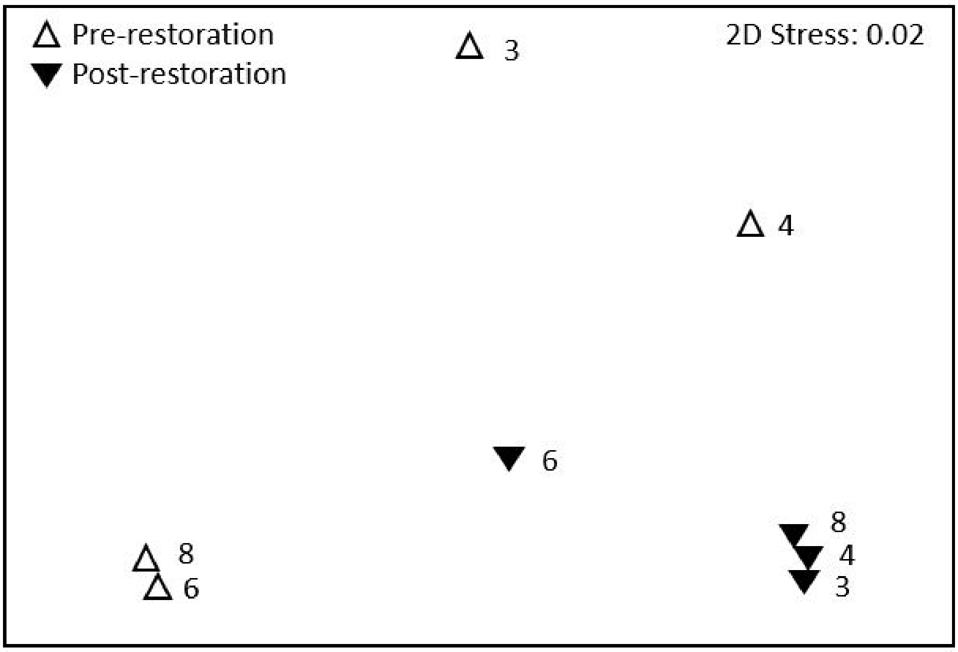

Figure 2. Non-metric multidimensional scaling plot showing fish community convergence between 1998 and 2007.

Table 1. Reaches occupied by species-age classes before habitat restoration (1998) and after habitat restoration (2007 and 2009). Bonneville cutthroat trout are not included in this table because they were not present in the entire section either before or after restoration. Presence is indicated with a 1 and absence with a 0. Reach 4 is the reference reach that was not channelized.

Reach, Year	Presence/Absence								Pre-Post Difference
Species	**8, 1998**	**8, 2007**	**6, 1998**	**6, 2009**	**4, 1998**	**4, 2007**	**3, 1998**	**3, 2007**	
Brown trout-Juvenile	1	1	1	1	1	1	1	1	0
Brown trout-Adult	1	1	1	1	1	1	1	1	0
Rainbow Rrout-Juvenile	1	0	1	0	1	0	0	0	-3
Rainbow Trout-Adult	1	0	0	1	1	0	1	1	-1
Redside Shiner-Juvenile	0	1	0	1	1	1	1	0	1
Redside Shiner-Adult	0	1	0	0	1	1	1	1	1
Mottled Sculpin-Juvenile	1	1	1	1	1	1	1	1	0
Mottled Sculpin-Adult	1	1	1	1	1	1	1	1	0
Mountain Whitefish-Juvenile	0	1	0	1	1	1	0	1	3
Mountain Whitefish-Adult	0	1	1	1	1	1	1	1	1
Utah Sucker-Juvenile	0	0	0	1	0	1	0	1	3
Utah Sucker-Adult	0	0	0	0	0	1	1	1	1
Mountain Sucker-Juvenile	0	1	0	0	0	1	0	1	3
Mountain Sucker-Adult	0	1	0	0	1	1	0	1	2
Speckled Dace-Juvenile	0	1	0	0	1	1	0	1	2
Speckled Dace-Adult	0	1	0	1	0	1	0	1	4
Longnose Dace-Juvenile	0	0	0	0	0	1	0	1	2
Longnose Dace-Adult	1	1	1	1	0	1	0	1	2
S. Leatherside Chub-Juvenile	0	0	0	0	0	0	0	1	1
S. Leatherside Chub-Adult	0	0	0	0	1	0	0	1	0

4. Discussion

Habitat restoration resulted in increased complexity of habitat [17], and overall, this led to increased pattern of coexistence between native fishes and introduced brown trout. Six of nine native species expanded their distribution following restoration. One possibility to explain this pattern is habitat-mediated coexistence [13,23]. Complex habitat structure and arrangement provides areas where small and vulnerable size classes of native fishes are somewhat isolated from large piscivorous brown trout [11]. In the middle Provo River small size classes of native species occupy shallow margins of the main channel, small side channels, or backwater and cutoff pools where the abundance of larger brown trout is reduced [13,17]. Other studies have documented similar patterns in other systems [23–25]. Some of the species age classes that expanded their distribution following habitat restoration are large-bodied and relatively invulnerable to brown trout predation (e.g., adult Utah sucker and adult mountain whitefish). Expanded distributions of these species and age classes may be in response to increased recruitment because of refuge habitat for more vulnerable juvenile size classes, or it may be a direct response to an increase in habitat availability and quality, independent of the prevalence of brown trout in the river. Utah suckers, in particular, are long-lived so the direct response to habitat availability may be most important in the first few years following restoration; whereas, the demographic response may be more important later as the restoration project matures.

The two native species unaffected by habitat restoration, Bonneville cutthroat trout and southern leatherside chub, were the two rarest species in the middle Provo River prior to restoration. Neither of these species was able to expand their distribution or establish viable populations after reintroduction attempts. Cutthroat trout compete directly with brown trout [12,26,27], and they do not seem to be able to maintain long-term populations in the presence of brown trout [28]. Successful establishment of Bonneville cutthroat trout via reintroduction appears to be dependent on absence or low abundance of brown trout. Southern leatherside chub are highly vulnerable to predation by brown trout [29,30]. Some cases of apparent habitat-mediated coexistence between southern leatherside chub and brown trout are known, but these cases are all in systems where brown trout densities are relatively low [30,31]. For example, in Lost Creek in the Sevier River drainage in south-central Utah, USA, southern leatherside chub coexist with brown trout populations in downstream areas where densities of brown trout are relatively low. However, southern leatherside chub do not persist in upstream reaches where brown trout are more prevalent [32]. Even with availability of more complex habitat, southern leatherside chub cannot coexist with a large and robust population of brown trout [30–32].

Brown trout experienced a large increase in population density in response to changes in flow regime. In quantitative surveys for brown trout conducted in the middle Provo River in 1997, brown trout biomass was low at 7 kg/ha in the channelized Reach 8, and 29 kg/ha in the un-channelized reference reach (Reach 4). In contrast, the biomass of brown trout in 2010 was estimated at 332 kg/ha in Reach 8 and 175 kg/ha in the reference site (Reach 4). Prior to restoration and the implementation of the minimum flow requirement, brown trout densities averaged about 500 fish per river km; whereas, after the minimum flow requirement was finalized in 2000 but still before restoration was completed, brown trout densities averaged about 1250 fish per river km [33]. Since 2000, brown trout have comprised about 70% numerically of all fish captured in electrofishing surveys [17,33]. This increase in population is most likely a direct response to the minimum flow requirement taking effect because the increase in abundance and biomass was observed even before the restoration project was completed in all surveyed reaches [17,33].

In conclusion, the Provo River Restoration Project created more complex habitat throughout the middle Provo River compared to the river's highly channelized condition prior to restoration [17]. The increase in complex habitat was associated with an increase in the distribution of most, but not all, of the river's native fish species. Perhaps the strongest effect of the restoration was the dramatic increase in brown trout abundance and biomass following the establishment of a minimum flow requirement for the river. This large response in the brown trout population may be a primary reason that reintroductions of Bonneville cutthroat trout and southern leatherside chub were not successful [32]. Based on these results, the Provo River Restoration Project succeeded in creating a more natural fish community structure, but habitat-mediated coexistence was only partially successful and did not improve the status of the river's two rarest native fish species. It may be that habitat restoration in the presence of invasive species, may only be completely successful in terms of restoring native communities when the abundance of invasive species can be kept at low levels.

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Author Contributions: M.C.B. and B.R.M. conceived and designed the experiments; M.C.B., E.J.B. and C.E. performed the experiments; M.C.B., E.J.B. and C.E. analyzed the data; B.R.M. contributed reagents/materials/analysis tools; M.C.B. and C.E. wrote the paper.

Conflicts of Interest: The authors declare no conflict of interest.

Abbreviations

The following abbreviations are used in this manuscript:

ANOSIM	analysis of similarity
NMDS	non-metric multidimensional scaling

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