Non-native trout limit native brook trout access to space and thermal refugia in a restored large-river system

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We used direct observation via snorkeling surveys to quantify microhabitat use by native brook (Salvelinus fontinalis) and non-native brown (Salmo trutta) and rainbow (Oncorhynchus mykiss) trout occupying natural and restored pool habitats within a large, high-elevation Appalachian river, United States. Permutational multivariate analysis of variance (PERMANOVA) and subsequent two-way analysis of variance (ANOVA) indicated a significant difference in microhabitat use by brook and non-native trout within restored pools. We also detected a significant difference in microhabitat use by brook trout occupying pools in allopatry versus those occupying pools in sympathy with non-native trout—a pattern that appears to be modulated by size. Smaller brook trout often occupied pools in the absence of non-native species, where they used shallower and faster focal habitats. Larger brook trout occupied pools with, and utilized similar focal habitats (i.e. deeper, slower velocity) as, non-native trout. Non-native trout consistently occupied more thermally suitable microhabitats closer to cover as compared to brook trout, including the use of thermal refugia (i.e. ambient–focal temperature >2°C). These results suggest that non-native trout influence brook trout use of restored habitats by: (1) displacing smaller brook trout from restored pools, and (2) displacing small and large brook trout from optimal microhabitats (cooler, deeper, and lower velocity). Consequently, benefits of habitat restoration in large rivers may only be fully realized by brook trout in the absence of non-native species. Future research within this and other large river systems should characterize brook trout response to stream restoration following removal of non-native species.

Key words: habitat restoration, microhabitat use, non-native trout, Salvelinus fontinalis, snorkeling surveys, thermal refugia

Implications for Practice

- Non-native species appear to displace brook trout from restored large-river habitats.
- Effectively restoring brook trout habitat within large rivers will require minimizing or eliminating use of restored habitats by non-native species.
- Management of non-native species will become increasingly critical to the success of large-river habitat restoration as climate change further reduces habitat suitability and exacerbates interspecific interactions.

Introduction

Large-river systems are critical to the persistence of brook trout (Salvelinus fontinalis) metapopulations by serving as both supplemental foraging habitat (Petty et al. 2012; Petty et al. 2014) and dispersal corridors among tributary spawning habitats (Petty et al. 2005; Aunins et al. 2015). However, brook trout have been widely extirpated from large fluvial systems owing to anthropogenic habitat degradation and stream warming (Hudy et al. 2008; Petty et al. 2014). Thus, many brook trout populations currently exist within isolated tributaries, increasing their susceptibility to local extirpation (Letcher et al. 2007). Furthermore, many large-river systems throughout the native brook trout range also support non-native brown (Salmo trutta) and rainbow (Oncorhynchus mykiss) trout, which compete with brook trout for optimal habitat and alter their distribution (Wagner et al. 2013; Hitt et al. 2017). Climate change is expected to result in further loss of suitable large-river habitats because of increasing air temperature and altered hydrologic regimes (Flebbe et al. 2006; Merriam et al. 2017)—changes which can also increase suitability for non-native species.

Successful conservation of brook trout metapopulations will require protecting and restoring suitable large-river habitats. Previous studies have documented direct benefits of in-stream habitat enhancement, such as habitat restoration structures (Van...
Zyll de Jong & Cowx 2016), chemical remediation (McClurg et al. 2007; Watson et al. 2017), and riparian restoration (Sievers et al. 2017). However, evidence of positive brook trout response to restoration is mixed, particularly for physical habitat enhancement (see Whiteway et al. 2010). Variability in observed response can often be attributed to other limiting factors operating across multiple spatial and temporal scales (Pett et al. 2012). For example, habitat enhancement can have positive effects on non-target species (Cowx & Van Zyll de Jong 2004), ultimately having the potential to harm target species through increased competition for space or resources. To our knowledge, no study has assessed brook trout use of restored habitats within the context of potential benefits to non-native salmonids. This represents an important knowledge gap, because it will determine whether future habitat restoration projects produce benefits to brook trout or whether such efforts will have unexpected deleterious effects.

We provide an assessment of habitat use by native brook and non-native brown and rainbow trout within the upper Shavers Fork—a restored Appalachian large-river system that contains one of only a few documented networked and genetically mixed brook trout metapopulations (Aunins et al. 2015). Acid precipitation, as well as sediment deposition and channel and riparian modification associated with the timber industry, diminished habitat suitability and connectivity during the twentieth century (Pett et al. 2005). Efforts to remediate acid precipitation within tributary spawning habitats (McClurg et al. 2007) and restore connectivity through culvert removal (Wood et al. 2018) have been extremely successful. Following these successes, a four-and-a-half-mile habitat restoration project was completed within the Shavers Fork main stem in 2012. The habitat restoration effort was designed to increase suitable brook trout habitat (i.e. deep, high-velocity habitats adjacent to cover; Hansbarger et al. 2008) and availability of thermal refugia through creation of deep pools (Pett et al. 2012). The overarching goal of our research is to better understand how watershed restoration can be used to offset potential impacts to brook trout from expected climate-induced habitat loss. Our specific objectives in this study were to: (1) compare microhabitats occupied by brook, rainbow, and brown trout within natural and restored pool habitats, and (2) determine if the presence of non-native salmonids alters brook trout microhabitat use and response to the main-stem habitat restoration.

**Methods**

**Study Area**

The upper Shavers Fork is a high-elevation (originates at 1,300 m), 156 km² watershed located within the Monongahela National Forest in east-central West Virginia (Fig. 1). The Shavers Fork is a tributary to the Cheat River in the upper Ohio River basin. Land cover is predominantly mixed deciduous-coniferous forest with abundant red spruce (Picea rubens). The watershed contains a variety of stream environments that range from high-gradient, cold-water tributaries to low-gradient and highly productive large-river (>100 km²) reaches (Pett et al. 2014). Previous studies have indicated that brook trout disperse widely within this watershed and use a range of tributary and main-stem habitats throughout their life history (Pett et al. 2005, 2012, 2014; Huntsman et al. 2016).

**Data Collection**

We used direct observation via snorkeling surveys to assess microhabitat use by brook, brown, and rainbow trout within 34 pools (18 natural and 16 constructed) distributed along 10 km of the Shavers Fork main stem (Fig. 1). All pools were surveyed a minimum of three times. Surveys were conducted during the spring and summer (June–July) of 2015 and 2016. All surveys were conducted during low-flow conditions (between 0.71 and 1.55 m³/s) as measured by the USGS gauging station (station #03067510) located on Shavers Fork (Fig. 1). Mean of monthly discharges for June and July across the entire period of record (i.e. 2002–2016) are 3.43 and 2.83 m³/s, respectively. Highly variable flows during the 2015 sampling season limited the number of possible sampling events and observations. Therefore, only data collected during 2016 are considered further.

We entered the downstream end of each pool and waited for a minimum of 10 minutes to ensure any disturbed fish resumed normal behavior. We slowly moved toward the front of the pool and from one bank to another to ensure the entire pool was fully surveyed. We marked focal positions occupied by each observed individual with a numbered, weighted bobber adjusted to the approximate focal depth. Focal positions were recorded for individuals that maintained a single position for more than 10 seconds. We visually estimated the length of each trout using a measuring rod as a calibration tool (O’Neal 2007). After snorkeling the entire reach, we obtained the following measurements at each focal position: depth (cm), focal channel velocity (FCV; m/s), maximum channel velocity within a 60-cm radius (MCV; m/s), difference between MCV and FCV (i.e. ΔCV; m/s), distance to fish cover (i.e. any object capable of concealing a 15–20-cm fish; Petty et al. 2001; DFC; m), and focal temperature (°C). We calculated the difference between ambient and focal temperatures (i.e. ambient–focal; ΔT). Ambient temperature was determined by averaging across 10 randomly selected locations throughout each pool. We noted if each focal position represented a thermal refuge (i.e. ΔT >2°C; Torgersen et al. 2012).

Following each survey, we collected data on habitat availability from pools where trout were observed. We established transects every 5 m along the length of each pool and collected the following measurements at five evenly spaced points along each transect: total depth (cm), average channel velocity (60% total depth; ACV), MCV, and DFC (Petty et al. 2001). Initial availability data were collected following the first survey. Additional availability data were collected when discharge during subsequent surveys differed by more than 0.56 m³/s. We combined all availability data for each pool to ensure the full range of microhabitat characteristics available at the time of each survey and during the range of summer low-flow conditions was represented.

**Trout response to restored habitats**

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Figure 1. Location of the upper Shavers Fork (uSF) watershed (WS) within West Virginia. Survey locations and associated pool type are shown. Location of the U.S. Geological Survey (USGS) gauging station on Shavers Fork is also shown.
Microhabitat Availability and Use Within Natural and Constructed Pools

We used one-way permutational multivariate analysis of variance (PERMANOVA, 999 permutations, Euclidean distances) and subsequent one-way analyses of variance (ANOVA) to test for and characterize differences in microhabitat availability (depth, ACV, MCV, ΔCV, and DFC) between natural and constructed pools.

We used one-way PERMANOVA and subsequent pairwise comparisons to test for overall differences in focal microhabitat use (depth, FCV, MCV, ΔCV, DFC, and ΔT) among species (i.e. brook, brown, and rainbow trout). We used two-way PERMANOVA (999 permutations, Euclidean distances) to test for effects of species, pool type (i.e. natural and constructed), and their interaction on focal habitat use. We conducted two-way ANOVAs and associated Tukey pairwise comparisons to characterize significant differences in individual microhabitat characteristics within and among species between pool type.

Effect of Non-natives on Brook Trout Microhabitat Use

We used two-way PERMANOVA (999 permutations, Euclidean distances) to test for overall differences in focal microhabitat use (depth, FCV, MCV, ΔCV, DFC, and ΔT) by brook and non-native trout occupying pools alone (i.e. in allopatry) and in combination (i.e. in sympatry). We used two-way ANOVAs and Tukey pairwise comparisons to test for differences in individual microhabitat characteristics within and between species (i.e. brook and non-native trout) across occupancy category (i.e. allopatry and sympatry). We used Welch’s two-sample t tests to test for differences in length of sympatry and allopatric brook and non-native trout.

All analyses were performed in R 3.4.2 (R Core Team 2017). PERMANOVAs and associated pairwise comparisons were performed using functions adonis.ii and pairwise.perm.manova in package RVAideMemoire (Herve 2018). We performed two-way ANOVA using function Anova in package car (Fox & Weisberg 2011). We set α = 0.1 due to low sample size within and among species and pool type; however, we distinguish significance at α = 0.1 from that at α = 0.05.

Results

Microhabitat Availability and Use Within Natural and Constructed Pools

Microhabitat availability differed significantly between natural and constructed pools (one-way PERMANOVA, \(F_{[1,546]} = 11.1, p < 0.05\)). Microhabitats within constructed pools were deeper (one-way ANOVA, \(F_{[1,546]} = 11.2, p < 0.05\)) and closer to cover (\(F_{[1,546]} = 4.21, p < 0.05\)) with slower ACV (\(F_{[1,546]} = 8.40, p < 0.05\)) and MCV (\(F_{[1,546]} = 7.46, p < 0.05\)) (Table S1, Fig. 2).

We obtained focal microhabitat use for a total of 54 trout, including 21 brook, 20 brown, and 13 rainbow trout. Thirty-three trout (11 brook and 22 non-native) occupied natural pools, while 21 (10 brook, 11 non-native) occupied constructed pools. Focal microhabitat characteristics differed significantly between species across all pools (one-way PERMANOVA, \(F_{[2,51]} = 12.2, p < 0.05, \) Table S2), with brook trout occupying significantly different microhabitats than both brown and rainbow trout (subsequent pairwise comparisons indicated \(p < 0.05\)). There was no difference in focal habitats used by brown and rainbow trout across all pools. Therefore, we grouped brown and rainbow trout (i.e. non-native trout) for subsequent analyses.
Trout response to restored habitats

Figure 3. Box plots comparing depth, FCV, maximum channel velocity within a 60-cm radius (MCV), and difference between MCV and FCV (ΔCV) between brook and non-native trout occupying constructed (n = 10 and n = 11, respectively) and natural (n = 11 and n = 22) pools. Letters denote significant pairwise comparisons. All differences were significant at α = 0.05.

Table type (i.e. natural and constructed) modulated differential microhabitat use between species (i.e. brook and non-native trout) as indicated by significant species by pool type interactions via two-way PERMANOVA (F[1,50] = 9.6, p < 0.05, Table S3) and ANOVA (depth (F[1,50] = 9.6, p < 0.05), ACV (F[1,50] = 3.4, p < 0.05), MCV (F[1,50] = 5.3, p < 0.05), and ΔCV (F[1,50] = 3.4, p < 0.05), Table S4). Non-native trout occupied deeper microhabitats with slower FCV, MCV, and ΔCV than brook trout in constructed pools—a pattern not observed in natural pools (Table S5, Fig. 3). Brook trout occupying constructed pools utilized focal habitats with faster MCV and greater ΔCV than brook trout occupying natural pools and non-native trout occupying constructed and natural pools (Table S5, Fig. 3). We also observed significant differences in focal ΔT (F[1,50] = 6.60, p < 0.05) and DFC (F[1,50] = 7.47, p < 0.05) between brook and non-native trout; however, this pattern was not mediated by pool type (Table S4, Fig. 4). No brook trout were observed utilizing thermal refugia (i.e. ΔT > 2°C); however, four non-native trout (three brown and one rainbow) were observed utilizing these cooler areas. The highest observed focal temperatures utilized by a brook and non-native trout were 25.0 and 23.9°C, respectively.

Effect of Non-natives on Brook Trout Microhabitat Use

Occupancy category (i.e. allopatric brook trout, n = 11; allopatric non-native trout, n = 19; sympatric brook trout, n = 10; and sympatric non-native trout, n = 14) modulated differential focal habitat use between species as indicated by significant species by occupancy category interactions via PERMANOVA (F[1,50] = 10.4, p < 0.05, Table S2) and ANOVA (depth (F[1,50] = 10.4, p < 0.05), ACV (F[1,50] = 5.8, p < 0.05), MCV (F[1,50] = 23.3, p < 0.05), and ΔCV (F[2,48] = 15.9, p < 0.05), Table S6). Allopatric brook trout used significantly (Tukey pairwise comparisons, p < 0.05) shallower focal locations with faster FCV, MCV, and ΔCV as compared to sympatric brook and sympatric and allopatric non-native trout (Table S7, Fig. 5). Sympatric brook trout occupied focal habitats with similar FCV, MCV, ΔCV as compared to both sympatric and allopatric non-native individuals. Allopatric non-native trout occupied deeper habitats than both sympatric brook and non-native trout (Table S7, Fig. 5). Occupancy category had no effect on DFC or ΔT between species (Table S6). Sympatric brook trout were significantly larger than allopatric brook trout (t = -2.01, p < 0.1) (Fig. 6). There was no significant difference in the length of sympatric and allopatric non-native trout (t = 1.08, p > 0.1).

Discussion

Brook trout use of restored habitats within Shavers Fork appears to be altered by the presence of non-native species. Smaller brook trout avoided pools occupied by non-native...
Trout response to restored habitats

Figure 5. Box plots comparing depth, FCV, maximum channel velocity within a 60-cm radius (MCV), and difference between MCV and FCV (ΔCV) between brook and non-native trout occupying pools alone (n = 11 and n = 19, respectively) (i.e. allopatric) and in combination (n = 10 and n = 14) (i.e. sympatric). Letters denote significant pairwise comparisons. All differences were significant at α = 0.05.

Figure 6. Box plots comparing mean length of brook and non-native trout occupying pools alone (n = 11 and n = 19, respectively) (i.e. allopatric) and in combination (n = 10 and n = 14) (i.e. sympatric). Asterisks denote significant within-species pairwise comparisons.

trout, and they tended to use faster focal habitats further from cover than larger brook trout or non-native trout. In contrast, larger brook trout did not avoid pools with non-native trout and tended to use similar microhabitats as non-native trout. Non-native individuals consistently occupied cooler habitats than brook trout and were observed utilizing thermal refugia (i.e. ΔT >2°C), whereas no brook trout were observed utilizing these colder habitats. Together, these results suggest that non-native trout within Shavers Fork may influence the distribution of smaller brook trout via displacement and limit brook trout access to space, resources, and thermal refugia within restored main-stem habitats.

To our knowledge, this study represents the first to directly assess microhabitat use by brook and non-native trout within the context of stream restoration. Nevertheless, our results are generally consistent with previous studies documenting brook trout preference for shallow habitats near areas of high velocities (Fausch & White 1981) and brown trout preference for deeper habitats with slower velocities and ample cover (DeWald & Wilzbach 1992; Quinn & Kwak 2000). Our results also corroborate previous studies documenting altered focal habitat use by brook trout in the presence of (Öhlund et al. 2008; Hitt et al. 2017) and following the removal of (Fausch & White 1981) non-native salmonid species.

However, our study is unique in that it further suggests use of restored habitats by brook and non-native trout is modulated by individual size. Smaller brook trout tended to occupy constructed pools in the absence of non-natives, presumably allowing them to utilize focal positions further from cover that are more conducive to optimal foraging on drifting insects (i.e. faster velocities at the head of constructed pools; Hughes 1998). Both larger brook and non-native trout occupied deeper, lower velocity habitats that were also characterized by high densities of forage fishes (e.g. rosy side dace [Clinostomus funduloides], blacknose dace [Rhinichthys obtusus], and creek chub [Semotilus atromaculatus]). These habitats likely provide larger brook and non-native trout the opportunity for piscivory to meet their higher energetic demands and maximize individual growth (Jonsson et al. 1999; Huntsman et al. 2016). Overlap of habitat preferences between larger brook and non-native trout appears to suggest that larger brook trout can successfully compete with non-native individuals for preferred microhabitats within restored streams. However, numerous studies have documented longer-term consequences for brook trout occupying habitats sympatrically with non-native trout, including decreased growth rates (DeWald & Wilzbach 1992) and reproductive success (Sorensen et al. 1995).

Our results generally support recent laboratory studies documenting displacement of brook trout from thermal refugia in the presence of brown trout (Hitt et al. 2017). These results have important implications for brook trout within Shavers Fork and other systems where exceedance of recognized thermal criteria (Chadwick et al. 2015) limits brook trout exploitation of productive main-stem habitats (“temperature-productivity squeeze,” Petty et al. 2014). Our results further suggest that the presence of non-native trout exacerbates the “temperature-productivity squeeze” via competition for limited thermally suitable habitats. Reduced access to thermal refugia within Shavers Fork could have long-term impacts on the dynamics and success...
of the broader metapopulation. Interestingly, we consistently documented brook trout occupying habitats with temperatures exceeding the preferred thermal range for brook trout (8–21°C, Hartman & Sweka 2001). One brook trout was observed foraging at 25.0°C. To our knowledge, this represents the highest temperature at which brook trout have been observed foraging in a natural system.

There are several limitations to this study. Highly variable flows during the first summer of this study (2015) restricted data collection to a single summer (2016), limiting our overall sample size. Moreover, the scope of this study was limited to comparing constructed and natural pools. We chose to focus on pool habitats because they were specifically designed to increase the availability of physically and thermally suitable brook trout habitat within Shavers Fork. It is possible that interactions between brook and non-native trout within other habitat types (e.g. riffles or runs) are different (e.g. pattern or magnitude) than those observed within pools. Finally, it is possible that observed size-dependent habitat use by brook trout was due to preference rather than competitive exclusion by non-native salmonids. Distinguishing causal mechanisms for observed patterns in habitat use will require an experimental removal study to directly test the hypothesis that small brook trout are forced to use suboptimal (i.e. shallow, high velocity) habitats because of exclusion by larger competitors (see Petty & Grossman 2010). Despite these limitations, however, we identified significant patterns in habitat use consistent with previous studies characterizing direct effects of non-native species on brook trout distribution across multiple scales (Fausch & White 1981; Waters 1983; McKenna et al. 2013; Wagner et al. 2013; Hitt et al. 2017).

Perhaps the greatest strength of the current study is that it occurred after all other chemical and physical factors known to limit brook trout populations within the upper Shavers Fork watershed were addressed. Specifically, acid remediation in spawning tributaries has maximized watershed-scale recruitment and production (McCulog et al. 2007). Culvert replacements on several key tributaries have enabled dispersal among critical spawning tributaries (Poplar-Jeffers et al. 2009; Wood et al. 2018) and large river supplemental foraging habitats (Huntsman et al. 2016). Access to large-river habitats also alleviates density-dependent regulation within low-productivity tributary environments (Huntsman & Petty 2014; Petty et al. 2014). Thus, the current habitat restoration effort conforms to mounting calls for watershed-scale restoration programs that simultaneously address multiple limiting factors (Petty & Merrim 2012; Palmer et al. 2014). The success of any restoration effort, particularly in-stream habitat enhancement projects, will only be successful if other underlying factors are addressed.

Access to suitable large-river habitats may become even more limited as air temperatures increase as a result of climate change (Flebbe et al. 2006). Within Shavers Fork, previous research suggests large-river habitats will remain thermally suitable for brook trout owing to increased precipitation and associated discharges that offset the effects of increased air temperatures (Merriam et al. 2017). However, this study did not consider the effects of interspecific competition and interactions. Even slight warming may exacerbate interspecific interactions (Taniguchi et al. 1998) and increase the competitive advantage of non-native salmonids (Carlson et al. 2007; Öhlund et al. 2008), precluding brook trout from utilizing any or all thermally suitable microhabitats within Shavers Fork. Thus, current benefits of the restoration activities to brook trout may be completely lost due to climate change without a management system that addresses non-native salmonids.

The primary goal of the restoration effort was to increase the availability of microhabitats with the highest suitability for brook trout (i.e. deep, high-velocity areas adjacent to cover, Hantsberger et al. 2008), as well as the availability of thermal refugia (Petty et al. 2012). Significant differences in microhabitat characteristics between natural and constructed pools indicate habitat restoration within the Shavers Fork created distinct and novel habitats (i.e. deeper, slower velocity pools with greater cover availability). We provide evidence to suggest that non-native salmonids may limit access by smaller brook trout to these restored habitats, as well as displace small and large brook trout from optimal focal habitats (e.g. thermal refugia) therein. Furthermore, we found no difference in focal habitat use between brook and non-native trout within natural pools, suggesting interspecific competition for preferred focal habitats likely occurs throughout the Shavers Fork. Together, these results emphasize the need for restoration practitioners to consider the presence or absence of non-native species when prioritizing sites for brook trout habitat restoration projects, particularly when proposed restoration activities could benefit non-native populations. Restoration efforts within this and other large-river systems will need to include efforts to control non-native populations in order to fully realize benefits to native brook trout. This is particularly true within the context of climate change, which is expected to exacerbate brook trout interactions with non-native species.

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Supporting Information
The following information may be found in the online version of this article:

Table S1. Results of one-way analyses of variance testing for significant differences in available microhabitat characteristics between natural (n = 285) and constructed (n = 263) pools.

Table S2. Results of one-way permutation multivariate analysis of variance and subsequent pairwise comparisons testing for differences in focal microhabitat use among brook (BT), brown (BR), and rainbow (RB) trout.

Table S3. Results of two-way permutation multivariate analyses of variance testing for differences in focal microhabitat use among pool type (i.e. natural and constructed) and species (brook and non-native trout), as well as among occupancy category (i.e. sympatric and allopatric) and species.

Table S4. Results of two-way analyses of variance characterizing differences in focal microhabitat characteristics within and among species between pool type.

Table S5. Results of Tukey pairwise comparisons characterizing significant differences in focal microhabitat characteristics within and among species between pool type.

Table S6. Results of two-way analyses of variance characterizing differences in focal microhabitat characteristics within and between species across occupancy category (i.e. allopatry and sympathy).

Table S7. Results of Tukey pairwise comparisons characterizing significant differences in focal microhabitat characteristics within and among species between occupancy category (i.e. allopatry and sympathy).

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