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FEATURED PAPER

Evaluating the Trade-Offs between Invasion and Isolation for Native Brook Trout and Nonnative Brown Trout in Pennsylvania Streams

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Abstract

A popular conservation strategy for native trout species in western North America is to prevent invasions by nonnative trout by installing barriers that isolate native trout populations into headwater streams. In eastern North America, native Brook Trout *Salvelinus fontinalis* are frequently replaced in coolwater habitats by nonnative Brown Trout *Salmo trutta* and relegated to small headwater streams. In this study, we compared the effects of isolation and invasion by nonnative Brown Trout on the distribution and demographic structure of Brook Trout populations from 78 trout streams in northwestern Pennsylvania. The Brook Trout and Brown Trout distributions varied in predictable ways along the stream size gradient, with Brown Trout becoming dominant in larger streams. However, there was a prominent barrier effect, with streams 12 times more likely to have Brook Trout than Brown Trout when a downstream barrier was present between the sample site and the nearest Brown Trout stocking location. In comparison, 91% of the streams with Brown Trout had no downstream barrier, suggesting that barriers are important in creating refugia for Brook Trout. Brown Trout also appeared to have a negative impact on Brook Trout population demographics, as Brook Trout populations in sympatry with Brown Trout had fewer age-classes and lower population densities than allopatric Brook Trout populations. Isolating Brook Trout to small headwater streams with downstream barriers that prevent Brown Trout invasion could be a viable conservation strategy in regions where barriers would serve to reduce the negative impacts from Brown Trout. Since barriers could further fragment local Brook Trout populations, however, they would need to be strategically placed to allow for seasonal movements to maintain metapopulation structure and ensure population persistence.

A frequently documented pattern in North American streams is the gradual replacement of native trout *Oncorhynchus* and *Salvelinus* spp. with nonnative trout. However, it is often unclear whether this is due to replacement or displacement of the native species by a nonnative species. In some cases, nonnative trout replace native trout by filling open “ecological niches” in the wake of native extirpations resulting from land use changes and habitat degradation (Dunham et al. 2002; Rieman et al. 2006; Hudy et al. 2008; Al-Chokhachy et al. 2016). In other instances, nonnative trout have displaced native trout by directly reducing native population viability via hybridization (Allendorf and Leary 1988) or interference competition and intraguild predation (Fausch and White 1981; Grant et al. 2002; Peterson et al. 2004; Hoxmeier and Dieterman 2013; Hitt et al. 2017). Preventing the establishment of nonnative trout has been an important part of native trout conservation because native trout often recover following the removal of nonnatives (Kanno et al. 2016).

One management strategy for conserving native trout in the face of nonnative introductions has been the “isolation management” strategy, whereby barriers are intentionally installed to prevent invasion by nonnative trout (Novinger and Rahel 2003; Rahel 2013). An unfortunate

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consequence of this strategy is that native populations become isolated from each other, which can lead to a loss of genetic diversity, inbreeding depression (Wofford et al. 2005; Robinson et al. 2017), and the elimination of particular life history strategies (Peterson et al. 2008; Fausch et al. 2009). Understanding the costs associated with this trade-off is important for evaluating whether the benefits of reduced invasion are worth the risks from reduced genetic and life history diversity. This question is complicated by climate change, which can further reduce available habitat for native trout that are already isolated into small, headwater habitats (Wenger et al. 2011; Roberts et al. 2017). Fausch et al. (2009) emphasized two questions for evaluating this trade-off: (1) Are populations vulnerable to invasion? and (2) Would populations be threatened with extinction if isolated? Barriers are more appropriate for populations vulnerable to invasion, whereas maintaining connectivity is more appropriate for populations susceptible to the effects of isolation (Peterson et al. 2008).

In western North America, isolation management has been implemented for conserving native Cutthroat Trout *Oncorhynchus clarkii*, which can persist in isolated, headwater streams after downstream replacement by nonnative trout (Novinger and Rahel 2003; Peterson et al. 2008; Cook et al. 2010). We sought to explore whether this strategy could be applied to Brook Trout *Salvelinus fontinalis* in their native range of eastern North America, where a similar ecological scenario exists. Nonnative Brown Trout *Salmo trutta* frequently occur within the native range of Brook Trout, and both species represent important recreational fisheries (McKenna et al. 2013; Davis and Wagner 2016). It is well established that the two species replace each other along the longitudinal stream gradient, with Brown Trout dominating in larger, warmer reaches downstream and Brook Trout dominating in cold headwater reaches (Magoulick and Wilzbach 1998; Korsu et al. 2007; Ohlund et al. 2008; Wagner et al. 2013). It is also well documented that Brown Trout have pronounced negative impacts on both native trout and native nongame species, with Brown Trout being listed as one of the 30 most globally invasive fish species (reviewed in Budy and Gaeta 2017; see also McDowall 2006; Kirk et al. 2017).

Although these longitudinal patterns can be attributed to differences in physiochemical and thermal preferences (Taniguchi et al. 1998; Kocovsky and Carline 2005), the relegation of Brook Trout to headwater streams has also been attributed to displacement by Brown Trout in downstream reaches. Previous landscape-level studies have provided evidence that Brown Trout reduce the occurrence of Brook Trout at locations where they would otherwise be found (McKenna et al. 2013; Wagner et al. 2013; Kirk et al. 2017). Brown Trout grow faster (Carlson et al. 2007) and have superior competitive behaviors that give them an advantage over Brook Trout for habitat selection, except in the coldest headwater reaches (Fausch and White 1981; Ohlund et al. 2008; Hitt et al. 2017). Given the decline of Brook Trout populations in much of their native range from adverse land use impacts and climate warming (Meisner 1990; Hudy et al. 2008), it is important to consider alternative conservation strategies, especially in regions where the potential for displacement by nonnative trout is high (Kanno et al. 2016).

The objective of this paper was to evaluate the applicability of an isolation management strategy for Brook Trout conservation by describing the effects of Brown Trout and barriers on the distribution and demographics of Brook Trout populations in northwestern Pennsylvania. We hypothesize that protecting Brook Trout against invasion by Brown Trout is more important than protecting them against the negative demographic effects of isolation into small headwater streams. We made two predictions based on Fausch et al.'s (2009) questions about invasion susceptibility and persistence in isolation to test our hypothesis. For invasion susceptibility, we predicted that the presence of barriers would be positively associated with the presence of allopatric Brook Trout and negatively associated with the presence of allopatric Brown Trout. For persistence in isolation, we predicted that Brook Trout population demographics (using age structure and population density as surrogates for population persistence) would be negatively impacted by their occurring in sympatry with Brown Trout as opposed to their occurring in small, upstream locations (a proxy for low connectivity and network size).

METHODS

Study area.— Brown and Brook Trout populations were surveyed at 78 stream sites (a subset of the 295 sites surveyed for fish community studies in this region) of the upper Allegheny River basin of northwestern Pennsylvania from 2006 to 2016. Thirty-four (44%) of these sites were sampled in 2016 with the specific objective of evaluating the presence of trout in small streams with and without barriers after exploratory analyses (with data collected prior to 2016) suggested a possible barrier effect. Sites were selected within areas of known Brown Trout stocking and robustly distributed across three western subbasins of the upper Allegheny River basin: French Creek, Oil Creek, and Brokenstraw Creek (Figure 1). These three subbasins lie within the glaciated Appalachian Plateau region of Pennsylvania and represent the western fringe of the Brook Trout's native range in Pennsylvania (Figure 1). Streams in the northwestern corner of Pennsylvania traverse a mixed forest–agricultural landscape, becoming higher in elevation, higher in gradient, lower in alkalinity, and lower with respect to agricultural impacts toward the east (Whitney and DeCant 2003; Kirk et al. 2017). As a result, both species become more prevalent toward the east.

We restricted our analyses to trout populations found within small streams having watershed areas of 0.5–16 km^2, which is the size range in our study area in which both Brown and Brook trout have been observed (see also Kanno et al. 2015). Brown Trout are the dominant trout species in relatively large, coolwater streams in this region (16–35 km^2; see Kirk et al. 2017). Streams within the size range we studied have moderate to high gradients with substrates dominated by gravel and cobble, high levels of natural watershed forest cover, high riparian forest intactness, and cold instream temperatures. The native assemblages in these streams are typically dominated by only a few species, including Mottled Sculpin *Cottus bairdi*, White Sucker *Catostomus commersoni*, 2–3 cyprinid species *Rhinichthys* and *Semotilus* spp., and 2–3 darter species *Etheostoma* spp. Brown Trout are the only nonnative species in these streams, and naturally reproducing populations have been established in parts of our study region for at least 20 years based on long-term sampling (Wissinger and coworkers, unpublished data).

Fish sampling and population characteristics.— Trout populations were sampled following a methodology similar to that of Kirk et al. (2017), which we briefly describe here. Sampling was conducted with a pulsed-DC backpack electrofisher (Smith-Root) during base flow conditions from May to October. Although different movement patterns between Brook Trout and Brown Trout can affect detection probability during different seasons (Davis et al. 2015), surveys were pooled across seasons because a priori analyses revealed no seasonal differences in trout presence or abundance. Samples were collected within a 100–200-m reach, which varied depending on the size of the stream. Because reach length and the number of passes (one, two, or three) varied among sites, we standardized population density across all sites as the catch per unit of effort (CPUE) of trout in the first 100 m of the first pass. The number of age-classes was estimated across the entire reach to determine the presence of any new trout size-classes that may have been absent in the first 100 m due to differences in habitat availability.

The total length of each trout was measured to estimate size structure and age-classes for each population. Sites were only classified as “Brook Trout sites” if they had naturally reproducing Brook Trout populations (i.e., not stocked fish) based on the presence of either age-0 Brook Trout or more than two age-classes. In contrast, only a single Brown Trout of any size was required to be present for us to classify the site as a “Brown Trout site” (i.e., stocked or naturalized fish). Sympatric populations met both these requirements for each species. While some of the Brown Trout in these streams were likely to have been of stocked origin, we minimized the overlap with stocked Brook Trout by excluding locations that were upstream of Brook Trout stocking locations in the same watershed. Although these populations may have been stocked historically, they have been self-recruiting for a substantial

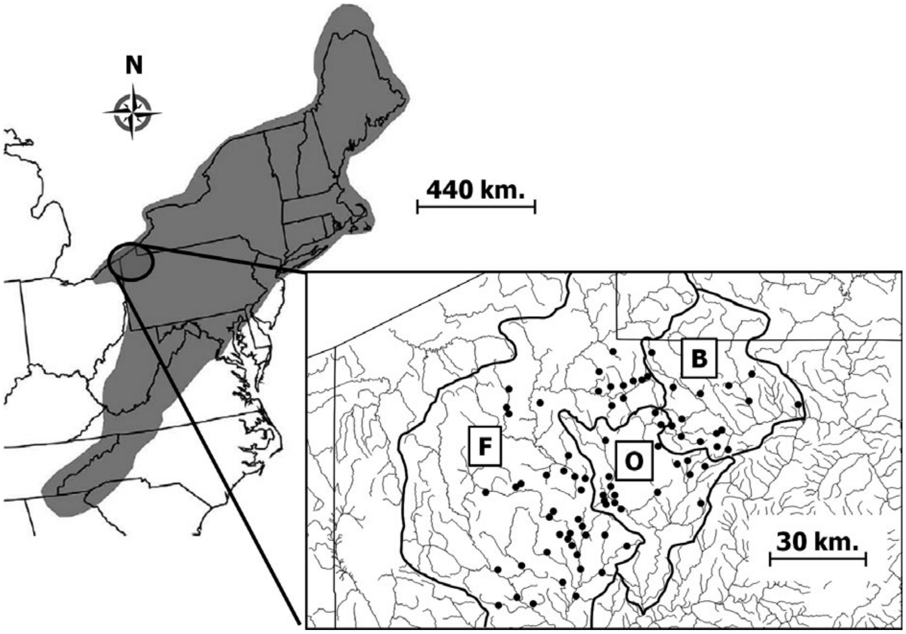

FIGURE 1. Locations of the 78 sampling sites in the upper Allegheny River basin (dots) and the historical range of Brook Trout (shaded area in the inset; from Hudy et al. 2008). Dark black lines outline the major study basins: French Creek (F), Oil Creek (O), and Brokenstraw Creek (B).

period of time based on comparisons with historical data (pre-1995; Argent et al. 1997).

Length-frequency histograms were constructed for 14 sites with Brook Trout population densities ≥20 individuals. Different age-classes were identified by visually identifying natural cutoffs at which peaks in the number of Brook Trout within a given size range were separated by gaps in the size distribution, and age designations were made for each of the 14 sites (see Figure A.1 in the Appendix for examples). After accounting for the sampling season (fall [September–October] versus spring [May–June]), five age demarcations were determined and the following age-classes were assigned: 0 (25–100 mm; $n = 12$), 1 (101–175 mm; $n = 12$), 2 (176–250 mm; $n = 7$), 3 (251–300 mm; $n = 2$), and 4 (300+ mm; $n = 2$). (The sample sizes [n] are the numbers of sites from which the age designations were made.) We conducted a literature search for size-at-age estimates of Brook Trout in their native range and found correspondences with our study for the age-0, age-1, and age-2 classes. Although we may have overestimated the sizes of age-3 and age-4 fish, the general age demarcations for these two groups indicate that they still likely represent two separate age-classes.

Environmental and barrier-related variables.— The environmental data for distinguishing between Brook Trout and Brown Trout streams consisted of eight landscape and water chemistry variables. Basin delineations and extraction of landscape data were performed within ArcGIS (ARCMAP by ESRI on ArcGIS Desktop 9.3.1). Landscape variables included site latitude, site longitude, elevation (m), stream gradient (m/km), upstream watershed area (km^2), stream position (%), and upstream forest cover (%). Stream gradient was calculated as the difference in elevation between the headwater source of the stream and the site location based on National Hydrography Data Set flowlines. Stream position was calculated as the ratio between the distance to the headwater source of the stream and the nearest location downstream where Brown Trout were stocked. The stocking locations of Brown and Brook trout were identified from Pennsylvania Fish and Boat Commission records (https://fbweb.pa.gov/stocking/TroutStockingDetails_GIS.aspx). High stream position values correspond to sites close to the headwater source of the stream and far away from the stocking of Brown Trout. Upstream land cover was calculated as the percentage of natural land use types (e.g., forest and wetlands) in the catchment upstream of each sample site. Alkalinity was the lone water chemistry variable considered and was collected under base flow conditions for all sites. Water temperature was not included due to seasonal variation in the collection of water chemistry data. Further details on watershed and riparian land use and water chemistry can be found in Kirk et al. (2017).

We identified two different types of barriers to trout movement within ArcGIS. Dams were the first and were identified using a national barrier data set (Ostroff et al. 2013) to determine whether any human-constructed dams were located between the sampling site and the nearest downstream stocking location for Brown Trout (all dam heights were ≥4 m). The second barrier type was wetlands and impounded stream habitats, which can be associated with beaver dams or changes of instream habitat that can serve as barriers to Brown Trout movement (Kemp et al. 2012; Lokteff et al. 2013). We identified wetlands or impounded stream habitats by examining USGS topographic quadrat maps in ArcGIS to determine whether large wetlands occurred between sampling sites and the nearest downstream location for stocking Brown Trout. As a conservative estimate of how large a barrier needed to be in order to impede Brown Trout movement, we required that wetlands classified as barriers be greater than 1 km in length.

Data analyses.— To identify the environmental differences between Brown Trout and Brook Trout streams, the eight landscape and water chemistry variables for each site were analyzed by means of principal components analysis (PCA) using the program R (version 3.3.2; R Development Core Team 2014). This analysis allowed us to eliminate collinearity among variables and condense the number of variables into a set of uncorrelated axes representing important environmental gradients. All variables were standardized to a mean of zero to normalize the variances for variables of different units. PCA axes with eigenvalues >1 were considered for subsequent analysis as potentially important environmental gradients. We used permutational analysis of variance (PERMANOVA; adonis function in R version 3.3.2) to test whether the differences between Brown and Brook Trout streams obtained from the PCA were significant. We tested for the assumption of homogenous dispersion among trout categories before analysis.

We tested the role of environmental gradients from the PCA versus the role of barriers for explaining the occurrence of Brook or Brown Trout populations using a multinominal logistic regression model (multinom function in R version 3.3.2) with three response categories (only Brook Trout populations present, only Brown Trout populations present, and sympatric populations). The four variables included in the model were the first three axes from the PCA (all eigenvalues were ≥1.32) and the presence or absence of barriers identified within ArcGIS (dams, impoundments, and wetlands). Collinearity of all variables in the multinomial models was at an acceptable level (all $r \leq 0.27$). We then used an information-theoretic approach (Burnham and Anderson 2002) to select the best model for explaining the importance of environmental factors versus the presence of barriers. Three a priori models were selected: the full model (the three PCA axes plus the presence of dams/wetlands), an environment-only model (the three PCA axes), and a barrier-only model (the presence of dams/wetlands). We selected the best model using Akaike's information criterion adjusted for small sample sizes (AIC_c) and ranked the models with respect to their ΔAIC_c values and model weights (w_i). The importance of the variables in the multinomial models was assessed by means of Wald's chi-square test ($\alpha < 0.05$) as well as by the estimation of odds ratios.

We then used one-way analysis of covariance (ANCOVA; $\alpha < 0.05$) to evaluate the importance of environmental factors versus the presence of Brown Trout on the potential persistence of Brook Trout populations. Population density (CPUE) and age structure were used as response variables to serve as proxies for the potential of Brook Trout populations to persist in isolation (with higher densities and more age-classes corresponding to higher probabilities of persistence). The ANCOVAs used PCA axis 1 as a predictor variable to control for differences in population density and age-classes along important environmental gradients that differentiated Brook and Brown Trout conditions, with trout population type (allopatric Brook Trout populations versus sympatric Brook and Brown Trout populations) as a covariate. The ANCOVA results were analyzed using generalized linear models (glm function; R version 3.3.2). Population density was fit with a Poisson distribution and a log-link function due to the right-skewed nature of the count data. Age structure was fit with a Gaussian (normal) distribution, given the normality of this data. Diagnostic tests of normality and homoscedasticity in model residuals indicated that these assumptions were not violated for either ANCOVA model.

Finally, we tested for spatial autocorrelation in the residuals of both the multinomial regression and ANCOVA analyses, as autocorrelation would violate the assumption of independence for regression models (Zuur et al. 2010). We calculated Moran's I (Moran.I function; R version 3.3.2)—a measure of how similar streams are based on their proximity—using the residuals for each model and an inverse weighted-distance matrix based on the latitude and longitude of each site. We found no evidence of spatial clustering for any models (all $P > 0.211$), and thus we did not need to account for autocorrelation within our model structure.

RESULTS

Principal components analysis (PCA) revealed environmental differentiation between Brown Trout and Brook Trout streams along the first PCA axis, with sympatric streams lying between the two (Figure 2). The first three axes of the PCA explained 71.1% of the cumulative variation among streams. The first axis explained 35.1% of the variance, and the PERMANOVA revealed significant differences in stream characteristics among trout categories (Global $R^2 = 0.38$, $P < 0.001$). Brook Trout streams were smaller in size, higher in elevation, and located farther east, occupied positions closer to the headwater source of the stream, and had higher stream gradients than Brown Trout streams (Figure 2; Table 1). These differences between Brook Trout and Brown Trout streams were predominately associated with the longitudinal stream gradient (i.e., stream size), with Brown Trout replacing Brook Trout along a gradient of increasing stream size (Figure 3). Interestingly, Brown Trout occupied high stream positions only in low-gradient streams (<34 m/km), whereas only Brook Trout occupied high stream positions in high-gradient streams (Figure 4). The second and third axes explained 19.5% and 16.5% of the variance, respectively, and neither axis was associated with differentiation between Brook Trout and Brown Trout streams (PERMANOVA; both $P > 0.14$).

Environmental characteristics associated with the longitudinal stream gradient and barrier types were both important determinants of whether streams contained Brook Trout or Brown Trout. The model selection procedure chose the full model with the PCA axes and the presence of barriers as the best model, with a ΔAIC_c value of 14.1 vis-à-vis the second-ranked model and a $w_i = 0.99$. Streams were four times as likely (based on odds ratios) to be Brook Trout streams than Brown Trout streams with each unit increase along PCA axis 1 ($\chi^2 = 4.09$, $P < 0.001$; Table 2) but not along PCA axis 2 ($\chi^2 = 1.42$, $P = 0.157$) or PCA axis 3 ($\chi^2 = 0.64$, $P = 0.520$).

There was a significant barrier effect ($\chi^2 = 2.49$, $P = 0.013$), in which half (50%) of all Brook Trout–only streams had a dam or wetland located between the site and the nearest location of Brown Trout stocking. Odds

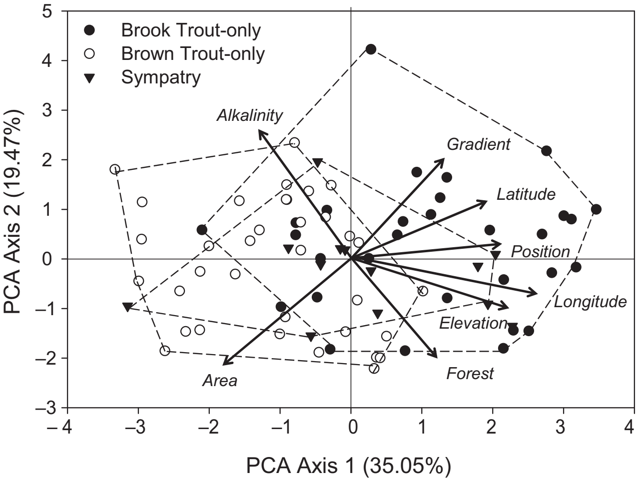

FIGURE 2. Results of a principal components analysis (PCA) characterizing eight environmental variables at the 78 study sites. Convex hulls are drawn around the Brook Trout–only streams, the Brown Trout–only streams, and streams with both species in sympatry.

TABLE 1. Mean (SD) landscape characteristics for the 15 Brook Trout streams with barriers, 15 Brook Trout streams without barriers, 35 Brown Trout streams, and 13 streams with Brook and Brown trout in sympatry across the study region.

Variable	Brook Trout streams with barriers	Brook Trout streams without barriers	Brown Trout streams	Sympatric streams
Sample size	15	15	35	13
Alkalinity	59.9 (32.1)	50.4 (37.4)	57.4 (26.2)	45.5 (19.1)
Watershed area (km^2)	3.4 (2.1)	5.2 (4.9)	8.3 (4.2)	5.0 (3.4)
Elevation (m)	433.5 (44.3)	445.7 (36.6)	396.4 (38.1)	414.1 (38.7)
Watershed forest cover (%)	75.0 (12.9)	71.4 (19.1)	64.7 (16.9)	72.7 (15.1)
Stream gradient (m/km)	31.4 (13.3)	25.7 (11.9)	16.8 (6.6)	24.5 (11.3)
Site latitude (°)	41.7 (0.1)	41.8 (0.1)	41.7 (0.1)	41.7 (0.1)
Site longitude (°)	−79.7 (0.1)	−79.6 (0.1)	−79.9 (0.1)	−79.7 (0.2)
Stream position	0.57 (0.25)	0.53 (0.29)	0.41 (0.24)	0.52 (0.21)

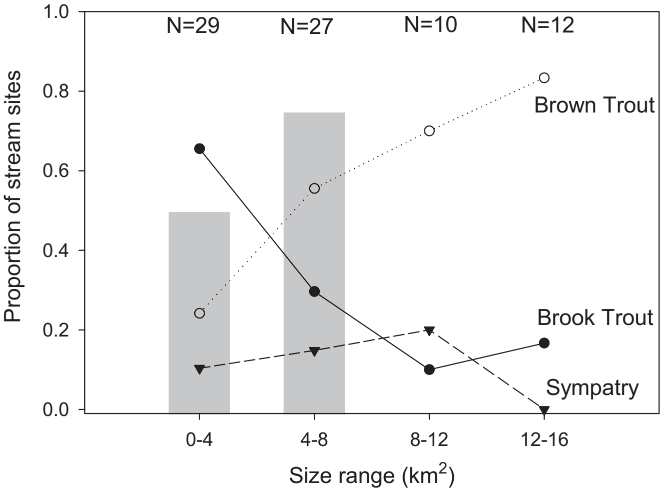

FIGURE 3. Relationships between the proportion of sites and stream size for the three trout populations. The gray bars show the proportion of Brook Trout–only streams in which a downstream barrier is present.

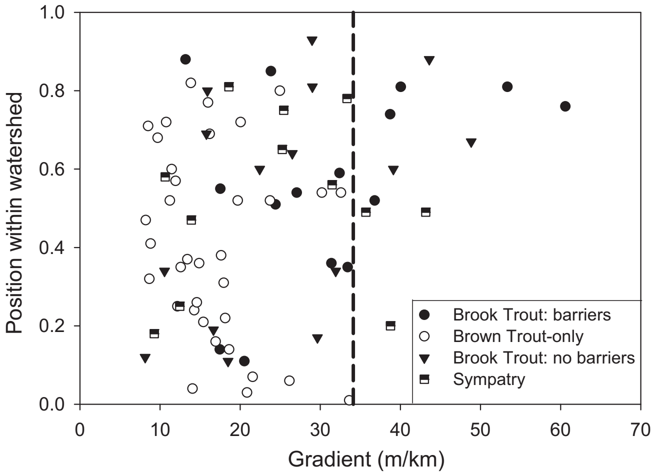

FIGURE 4. Relationships between stream position and stream gradient for Brook Trout–only streams (with and without downstream barriers), Brown Trout–only streams, and sympatric streams. The vertical dashed line represents the maximum gradient tolerable to Brown Trout, as estimated by the 95th percentile of the data from Brown Trout–only and sympatric streams.

ratios indicated that sites were 12 times as likely to have only Brook Trout when a barrier was present (Table 2). There were several notable differences in landscape-level characteristics between Brook Trout streams with and without barriers. Importantly, streams with barriers had smaller areas and steeper gradients than those without barriers (Table 1; Figure 4). In addition, barriers were present in 50% of Brook Trout streams in the 0–4-km^2 range and 75% of Brook Trout streams in the 4–8-km^2 range but were not present in the largest streams (Figure 3). In contrast, 91% of streams with Brown Trout had no such barriers and no sympatric populations had a barrier downstream.

Brook Trout population demographics were negatively impacted by the presence of sympatric Brown Trout but not by the longitudinal stream gradient associated with the first PCA axis (i.e., age and density were unaffected by fish's being in more upstream locations [both $P \geq 0.657$]). Although the overall Brook Trout age structure model was not significant (Gaussian GLM: $F_{2,\ 40} = 2.39$, $P = 0.105$), there was a significant covariate effect, with sympatric populations having fewer age-classes of Brook Trout (mean = 2.08) than allopatric Brook Trout streams (mean = 2.90; $P = 0.035$; Figure 5B). This reduction in age-classes was particularly noticeable for the age-0 class, which was 1.75 times less likely to be found in sympatric populations than allopatric Brook Trout populations. Brook Trout population density was also significantly lower for sympatric streams (mean = 9 fish/100 m) than for allopatric Brook Trout streams (19 fish/100 m; Poisson GLM: $P < 0.001$; Figure 5A).

TABLE 2. Multinomial logistic regression results testing the effects of environmental gradients (PCA axes) and barrier-related variables on the three different trout population types (Brook Trout only, Brown Trout only, and sympatry). Brown Trout–only streams were selected as the reference category. Values in bold italics are significant ($P < 0.05$).

	Brook Trout only			Sympatry		
Variable	χ^2	P-value	Odds ratio	χ^2	P-value	Odds ratio
PCA axis 1	***4.09***	***<0.001***	***4.09***	***2.68***	***0.007***	***2.15***
PCA axis 2	1.42	0.157	1.50	−0.24	0.812	0.93
PCA axis 3	0.64	0.520	1.25	***−2.16***	***0.031***	***0.46***
Barrier	***2.49***	***0.013***	***11.88***	−0.22	0.825	0.02

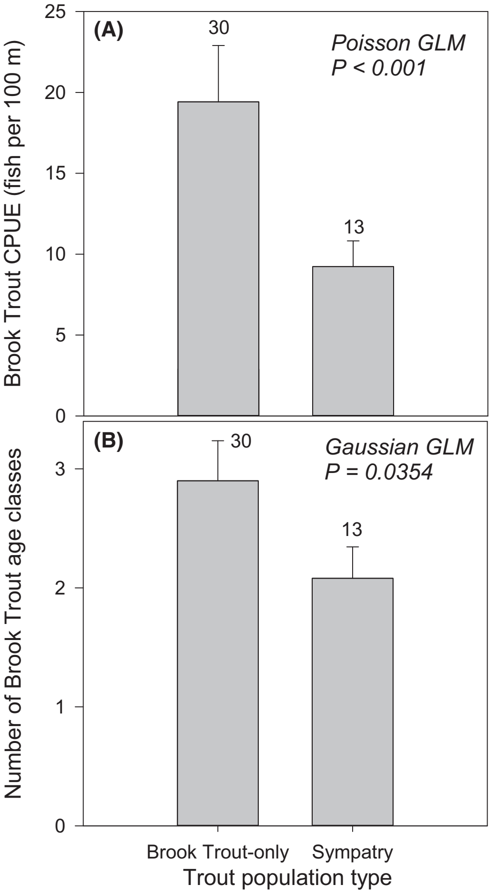

FIGURE 5. Results of analysis of covariance from generalized linear models (GLMs) for **(A)** Brook Trout population density and **(B)** the number of Brook Trout age-classes for Brook Trout–only and sympatric streams. The error bars are SEs; sample sizes are given above the bars.

DISCUSSION

Current priorities for Brook Trout restoration and conservation include maintaining genetic and life history diversity, removing dams, and reducing competition with nonnative trout from stocking (EBTJV 2011). Unfortunately, the strategies for addressing these different priorities can often conflict and differ in importance across the species' range. Managing for the improvement of population and habitat connectivity (i.e., preventing isolation) can increase the risk of interactions with invading nonnative trout (Peterson et al. 2008; Fausch et al. 2009). Previous studies examining this invasion–isolation trade-off have focused on native Cutthroat Trout in western North America, which are susceptible to displacement by nonnative Brook Trout and Brown Trout (Novinger and Rahel 2003; Peterson et al. 2008; Roberts et al. 2017). We can interpret our results in a similar way, in that our study involved a similar ecological scenario in which Brook Trout have been restricted to small, headwater streams and may have been displaced from suitable habitat by nonnative trout (Magoulick and Wilzbach 1998; McKenna et al. 2013; Wagner et al. 2013).

Many previous studies have noted a longitudinal pattern of zonation, with Brook Trout being concentrated in headwater reaches and Brown Trout dominating downstream (Figure 3; Magoulick and Wilzbach 1998; Weigel and Sorensen 2001; Korsu et al. 2007; Ohlund et al. 2008). Our findings are consistent with the results of these previous studies in that the first PCA axis revealed that Brook Trout are associated with smaller streams at higher elevations (Table 1), which often have more forest cover and colder instream temperatures (Wagner et al. 2013; DeWeber and Wagner 2015; Kanno et al. 2015). While this strong segregation along stream size gradients is in part a result of different physiochemical optima for temperature or oxygen (Taniguchi et al. 1998; Rieman et al. 2006), the degree to which these patterns can be attributed to species replacement from changing environmental conditions as opposed to species displacement due to competitive exclusion is often unknown (Al-Chokhachy et al. 2016).

We suspect that both replacement and displacement have contributed to this zonation pattern. Brown Trout likely filled the ecological niche that was available when Brook Trout were extirpated across much of their native range due to land use impacts and habitat degradation (Hudy et al. 2008). This is true for most of our study region, 50–80% of which was deforested in the 19th century, which would have resulted in a major loss of Brook Trout habitat (Whitney and DeCant 2003; Kirk et al. 2017). Although replacement may have been responsible for these patterns historically, our results indicate that population density and the number of age-classes of Brook Trout did not change along the first PCA axis, which is important in explaining the zonation patterns of Brook and Brown trout along the upstream-to-downstream gradient (Figure 2). Instead, Brown Trout in sympatry with Brook Trout had negative impacts on those demographic parameters (Figure 5). These results suggest that there is displacement when the species co-occur, which is consistent with previous evidence that nonnative Brown Trout negatively impact native species when they occupy the same habitats (McDowall 2006; Meredith et al. 2014; Kirk et al. 2017).

The ecomorphological similarity of these two species implies that they are likely to share similar niche characteristics that could lead to displacement (Petty et al. 2012; Davis and Wagner 2016). Brown Trout are the competitively dominant species and are thus capable of displacing Brook Trout from optimal foraging habitats and thermal refugia (Fausch and White 1981; Hitt et al. 2017), except in the coldest headwater streams (Korsu et al. 2007; Ohlund et al. 2008). Indeed, physiological differences can help mediate what would otherwise be asymmetrical interactions by giving each species ecological advantages under different conditions (Taniguchi et al. 1998; Hitt et al. 2017). It is important to note that the invasion process is composed of three steps: colonization, establishment, and impact (Dunham et al. 2002). Although we predominately evaluated the impacts from colonization and not those from establishment (i.e., any stream where Brown Trout were present), our results indicate that age-0 Brook Trout are less likely to be found in sympatric populations. Another study found that while adult Brook Trout (age-1 and older) were more likely to move upstream when in sympatry with Brown Trout, age-0 Brook Trout were not (Hoxmeier and Dieterman 2013). Interactions occurring at the age-0 Brook Trout–Brown Trout level might thus be important for explaining the patterns of replacement versus displacement of these two species.

When an isolation management strategy is deemed the best option for the conservation of native trout (i.e., the threat of displacement from nonnative trout is large), barriers are installed to prevent invasion. We found that large dams, wetlands, and impounded stream habitats were all correlated with the presence of Brook Trout and the absence of Brown Trout. Such features result in changes to instream habitat that may act as a barrier to Brown Trout movement, but the precise explanations remain unknown (Kemp et al. 2012; Lokteff et al. 2013). One potential explanation is a change in instream temperatures (e.g., beaver dams are likely to increase stream temperatures by converting lotic habitat to lentic habitat; Hudy et al. 2008). In any case, wetlands can serve as natural barriers that limit the upstream distribution of Brown Trout, and further research is warranted to understand exactly how they act as barriers.

Despite the benefits of shielding Brook Trout from the many ways in which nonnative Brown Trout can adversely impact them, isolation into small, disconnected populations can increase the risk of local extirpation. Two major factors will affect whether the isolation of Brook Trout in small headwater streams will be detrimental to their persistence. First, population persistence will depend on protecting streams against further habitat and thermal degradation, such as buffering them against the predicted increases in temperatures and flow intermittency associated with climate change (Carlson et al. 2015), minimizing the levels of landscape alteration (e.g., agricultural and urban development; Hudy et al. 2008; Wagner et al. 2013), and maintaining groundwater upwelling zones that create thermal refugia (Hitt et al. 2017). Restoration activities may also need to be implemented for populations when habitat quality is marginal. Unfortunately, these measures still do not protect populations from genetic drift, reduced resilience to stochastic events (Fausch et al. 2009; Roberts et al. 2017), and allele effects that can lead to population collapse when population size and genetic diversity are low (Post 2013).

The second factor is the ability to maintain a minimum network size that provides enough habitat volume to support a large, viable population while allowing for movement between subpopulations (i.e., the maintenance of metapopulation structure; Peterson et al. 2008; Aunins et al. 2015). A simulation study of Brook Trout in Massachusetts streams found that populations faced extirpation rapidly when barriers to movement were installed and the fish were isolated in small tributaries (Letcher et al. 2007). Inbreeding depression resulting from the loss of genetic diversity is a major consequence of fragmentation that can lead to extirpation, and gene flow is crucial for rescuing Brook Trout from inbreeding depression (Wofford et al. 2005; Robinson et al. 2017). However, the trade-offs between invasion and isolation will vary among regions, streams, and populations (Peterson et al. 2008; Fausch et al. 2009).

Brook Trout populations in the central, mountainous part of their native range often exist within large stream networks and exhibit movement patterns characteristic of a migratory life history strategy (Petty et al. 2012; Huntsman et al. 2016). Maintaining network connectivity for gene flow would be critical for Brook Trout viability under these circumstances (Davis et al. 2015). The barriers for Brook Trout in our study tended to already be associated with the smallest stream sizes (0–4 km^2), where Brown Trout were unlikely to invade (Table 1; Figure 3). Indeed, the presence and abundance of age-0 Brown Trout follows a pattern of increasing stream size (similar to Figure 3), and thus Brown Trout may be unable to establish populations in the smallest streams (Korsu et al. 2007; Ohlund et al. 2008). Although barriers might not be needed in the smallest streams, barriers in the next size range (4–8 km^2) are likely important for excluding Brown Trout from streams that they would be more likely to invade (Figure 3). A priori studies that consider network habitat size and movement rates for local populations should be important prerequisites for determining how to strategically position barriers that allow for seasonal movements among populations to help maintain genetic and life history diversity.

Although we did not directly address movement rates or metapopulation structure, anecdotal evidence suggests that many of these Brook Trout populations are already isolated and localized in small streams and unlikely to maintain connectivity with a larger metapopulation. Sampling downstream from a small subset of these populations ($n = 6$) on the same stream segment often reveals the disappearance of Brook Trout (see Table A.1). Additionally, 37% (11 of 30) of these Brook Trout streams are less than 5 km away from large streams (>100 km^2) that do not have Brook Trout and that are stocking sources of Brown Trout (Argent et al. 1997). Thus, installing barriers to Brown Trout invasion will unlikely exacerbate the costs of isolation already affecting these populations. On the other hand, these populations may have already suffered a substantial loss of genetic diversity due to severe isolation, and genetic rescues may be necessary to maintain them (Robinson et al. 2017). Climate change will further complicate this strategy by isolating Brook Trout populations into even smaller headwater locations and by increasing the ability of nonnative Brown Trout to expand upstream (Wenger et al. 2011; Roberts et al. 2017).

Given the threat that nonnative Brown Trout pose to native Brook Trout, our study provides an important framework for considering the implementation of isolation management strategies for Brook Trout in regions with landscape characteristics similar to those in our study. We found that the presence of Brown Trout in sympatry had negative impacts on Brook Trout population demographics (Figure 5), and that 50% of Brook Trout populations already reside above potential barriers. We suggest that isolation management is generally applicable for the conservation of Brook Trout in (1) low-gradient streams (<34 m/km; Figure 4) where strong elevation and temperature gradients that lead to strong zonation patterns are lacking, (2) relatively large (>4 km^2; Figure 3) headwater streams that Brown Trout can invade when barriers are absent, and (3) at the edges of their distribution, where populations have been greatly reduced (Hudy et al. 2008). In general, trout populations on the fringes of their distribution tend to be more prone to displacement by nonnative trout because habitat conditions are marginal for native species (Fausch 2008). Our conclusions are in agreement with the invasion-versus-isolation framework (Fausch et al. 2009), which concludes that a barrier to invasion will increase persistence when native populations are already highly isolated. The demographic parameters that we measured are only a proxy for persistence, and long-term monitoring that evaluates annual population variation in response to stochastic events (e.g., flow regimes) is needed to further support our assertion that isolation would not threaten persistence.

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Appendix: Additional Details on the Size Classification and Distribution of Brook Trout in the Study Streams

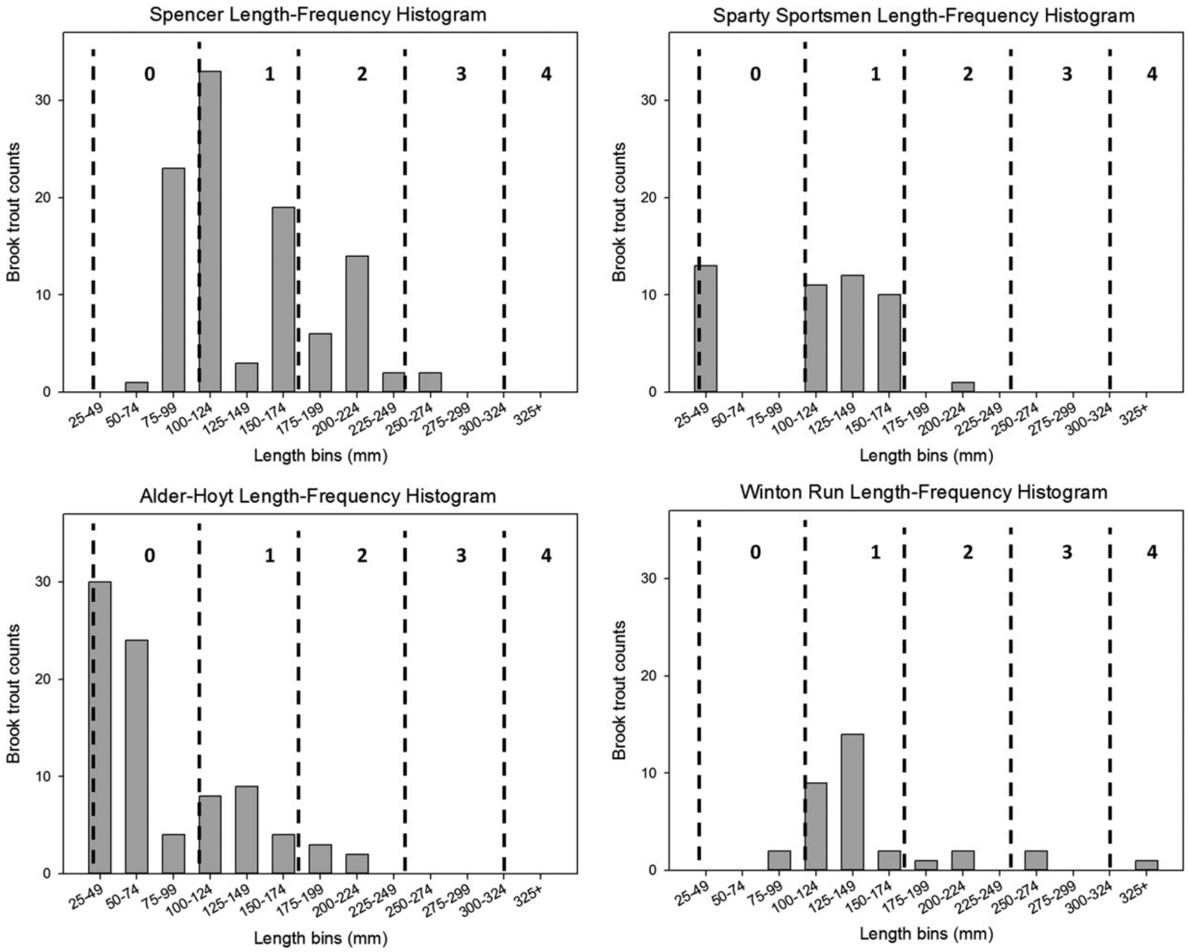

FIGURE A.1. Four examples from the 14 streams used to create length-frequency histograms for assigning different age-classes to Brook Trout. The first two represent a late-fall sample (Spencer) and an early-summer sample (Alder Hoyt), respectively. Note the shift in the age peaks for the fall sample due to a later sampling date. Fall samples made up a relatively small portion of the samples taken in Brook Trout streams (16%). The vertical lines and numbers 0–4 correspond to the age demarcations defined in the text.

TABLE A.1. Six examples of stream segments in which Brook Trout are present at an upstream site and not at a downstream site. The symbols used in the first column are defined as follows: * = streams with a downstream barrier to Brown Trout invasion; ψ = streams with naturalized Brown Trout present at the downstream site.

Stream	Distance between upper and lower sites (km)	Stream size increase from upper to lower sites (km^2)
Alder Run*	3.9	8.6
Hubbel Run*	4.1	17.2
Woodcock Creek*ψ	4.1	16.4
Pine Hollow Run	2.7	12.2
Irvine Runψ	3	17.4
Sugar Main*ψ	1.2	5.7