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ORIGINAL PAPER

Long-term population demographics of native brook trout following manipulative reduction of an invader

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Abstract Although laboratory studies have provided evidence for negative interactions between brook trout and brown trout, it is unknown how these interactions affect larger scale demographics in a natural setting. We tested the effects of invasive brown trout on brook trout demographics by removing brown trout from a sympatric population using a before–after control-impact study design. The study was conducted across a large stream network for a period of 6 years. Abundance of brook trout increased after brown trout removal primarily as a result of increased recruitment and immigration. Size structure also shifted towards larger individuals as a result of increased growth rates and a decrease in emigration of larger trout. Size at maturity and body condition did not change after brown trout removal. Adult brook trout survival increased during the post-treatment period in both the treatment and control reach. A decrease in flood intensity during the post-treatment time period may have led to increased survival. Adult survival may not be the best metric to use when assessing interactions between trout species, especially when the subordinate species has suitable areas to emigrate.

Keywords Competition · Salmonids · Forced emigration · Survival · Brook trout · Brown trout

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Introduction

Although interactions among salmonids has received considerable attention in both laboratory and field studies (see review by Hearn 1987), it is still unclear how population demographics are affected on a larger scale. While laboratory studies can lend insight to effects of competition on individuals, scaling these results to populations in natural systems can be problematic. For example, survival and growth of a subordinate species may decline when in confinement with a superior competitor, but if allowed to emigrate, such declines might not occur. Effects of a competitor may vary based on the temporal and spatial scale being examined. For trouts in streams, competition may only occur in specific areas of a stream during certain time periods and environmental conditions (Taniguchi and Nakano 2000). For example, it appears that brown trout *Salmo trutta* and brook trout *Salvelinus fontinalis* have a competitive advantage over cutthroat trout *Oncorhynchus clarkii* only at lower elevations in mountainous streams (Budy et al. 2008). Competition usually does not occur throughout the year, but rather during a critical time period either ontogenetically or seasonally, such as when prey or spawning habitat is limiting (Hearn 1987). For example, brook trout have the largest competitive advantage over cutthroat trout as juveniles, whereas competition at the adult stage can be minimal (Peterson et al. 2004). Because of the myriad of pathways in which competitors can interact, studies need to be conducted at temporal and spatial scales sufficient to encompass natural variability and environmental conditions.

In the Midwestern United States, native brook trout are typically found in lower abundance than introduced brown trout. While much of this has to do with the successful management of brown trout by fisheries management agencies, the recent discovery of remnant brook trout populations has given these same agencies renewed interest in conserving brook trout throughout the region (Hoxmeier et al. 2015). Because of their greater tolerance of degraded stream conditions, brown trout were favored over brook trout by fisheries agencies. However, improvements in watershed and riparian areas in many parts of the Midwest have made brook trout management a viable option once again (Hoxmeier et al. 2015). Conservation of remnant brook trout populations has become a priority, but increasing abundance of naturalized brown trout has made this management strategy challenging.

Similar to other invaded salmonid systems, brook trout in the Midwest are characterized by small populations confined to headwater reaches of streams with brown trout occupying middle and lower portions (Weigel and Sorensen 2001). Whether this is caused by competitive exclusion or inherent longitudinal habitat differences is poorly understood (Magoulick and Wilzbach 1998). It is unclear whether brook trout would inhabit the lower portions of streams in the absence of brown trout, or whether habitat limitations would still preclude them from these areas. If brown trout are filling an available niche, then they should not have any effect on the distribution and abundance of brook trout; therefore management focus should be on habitat rehabilitation as opposed to competition with a nonnative trout species. However, if brown trout are limiting brook trout survival and movement, then any attempts at restoring brook trout populations should include the reduction of brown trout.

Removal of brown trout should allow brook trout to use more favorable feeding sites (Fausch and White 1981); however, it is unknown what sort of population effects this would have. Growth of brown trout is often faster than brook trout when they occur in sympatry, but whether this is a result of competition or inherent growth rates is unclear (Carlson et al. 2007). Results from laboratory studies comparing growth rates between brook trout and brown trout are inconclusive, potentially the result of being confined in an artificial setting (DeWald and Wilzbach 1992). We would expect increased growth rates and size structure of brook trout following removal of brown trout if competition is occurring.

In this study, we conducted an experiment to test a set of hypotheses based on previous work examining brook trout demographics in sympatry with brown trout (Hoxmeier and Dieterman 2013). We hypothesized that brown trout were negatively effecting growth and movement of brook trout in Minnesota streams and that stream habitat was not limiting their populations. We predicted that brook trout would respond in several ways to brown trout removal. Increased survival and recruitment, and decreased emigration should lead to increased brook trout abundance, whereas increased growth and survival should lead to increased size structure after removal of brown trout. We tested the effects of non-native brown trout on a native brook trout population using a before–after control-impact (BACI) study design. Specifically, we monitored age specific survival, growth, emigration, recruitment, and abundance of individually tagged brook trout before and after a brown trout removal program in a large contiguous stream network for a period of 6 years.

Materials and methods

Study area

We chose a treatment and control reach on two southeastern Minnesota streams that had sympatric brook trout and brown trout populations to examine the effects of brown trout on growth, survival, and movement of brook trout (Fig. 1). Hemmingway Creek (control) is 3.2 km in length and flows into Pine Creek, a larger 4th order stream 28 km in length. Coolridge Creek (treatment) is a small stream 1.6 km in length and also flows into Pine Creek, 0.4 km downstream from the mouth of Hemmingway Creek. We sampled Pine Creek for presence of tagged brook trout throughout the study, but very few were encountered and therefore we did not include Pine Creek in any analyses for movement or survival. Watersheds are primarily a mix of hardwood forests, pasture, and row crop agriculture.

Brown trout were more abundant in downstream reaches of both Hemmingway and Coolridge creeks

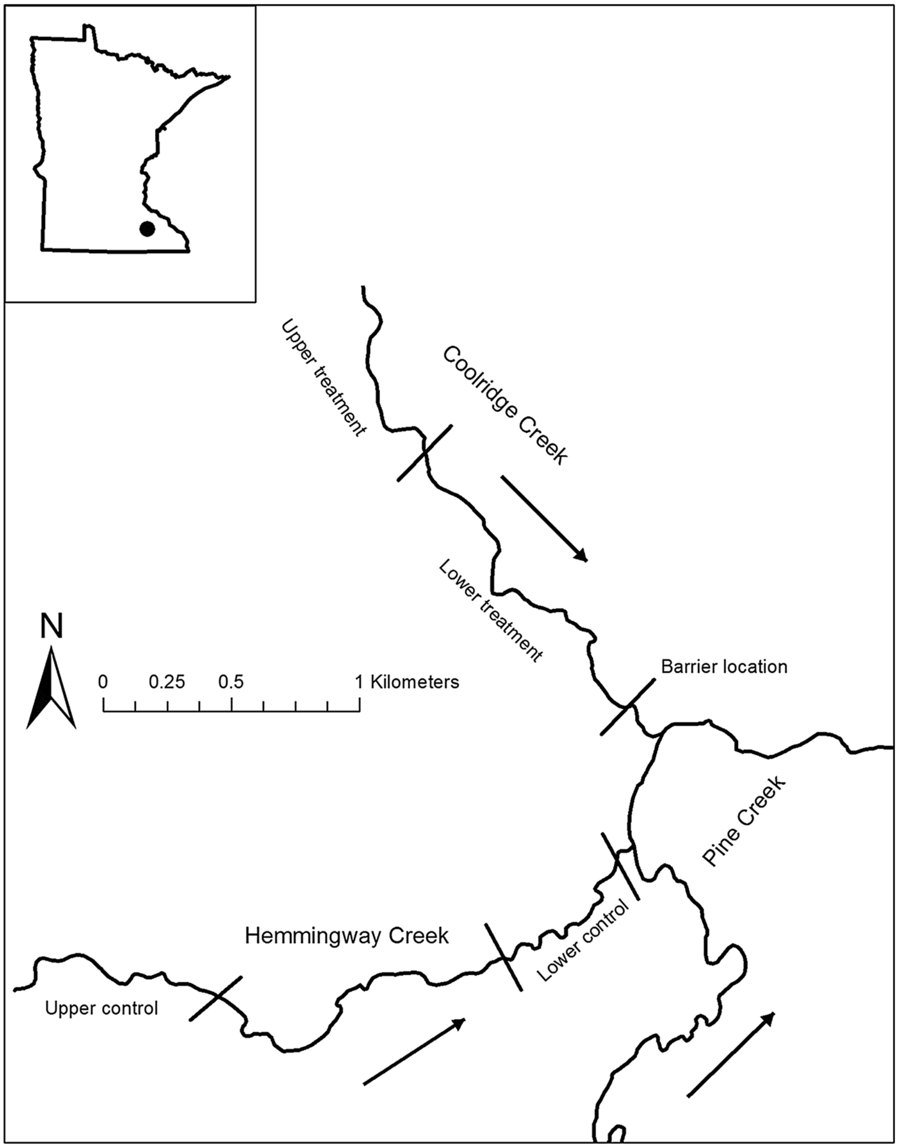

Fig. 1 Coolridge, Pine and Hemmingway creeks in southeastern Minnesota. *Brown trout* were removed from Coolridge Creek after a barrier was installed in 2009. *Arrows* indicate direction of stream flow

(Table 1). Therefore, we expected effects of brown trout removal to be greatest in the lower 1085 m of Coolridge Creek. Upstream from that point, brown trout were not as abundant and effects should be lessened. We used a brown trout dominated portion of Hemmingway Creek as our control reach (935 m) to compare with lower Coolridge. Upper portions of both streams were sampled to monitor movement in and out of our treatment and control reaches. We sampled 730 m in upper Hemmingway and 515 m in upper Coolridge. Water temperature was recorded every half hour in each stream reach with continuous temperature loggers. Water temperatures were similar in lower Coolridge and upper Hemingway, whereas in summer, lower Hemmingway was the warmest reach and upper Coolridge was the coldest reach (Table 1). Baseflow discharge measurements were taken with a Marsh-McBirney electromagnetic flow meter in each reach. Daily discharge data were gathered from a USGS gaging station in the Root River, 34 km downstream of the study site. Three major flooding events occurred during the pre-treatment time period, whereas, fewer and less intense flooding events occurred during the post-treatment period (Fig. 2).

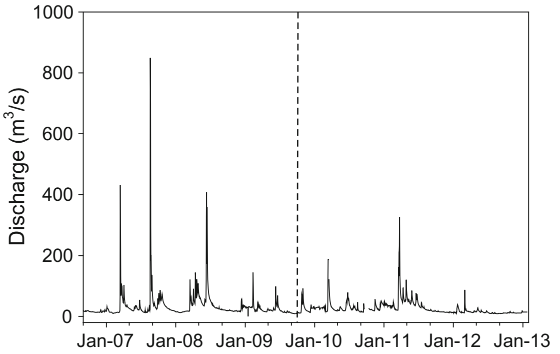

Fig. 2 Daily discharge from the Root River located 34 km downstream from the study area. *Dashed line* represents the beginning of *brown trout* removal in Coolridge Creek

Fish sampling and brown trout removal

Trout were sampled on 19 occasions from September 2006 through October 2012. We chose to sample 3 years prior to and after brown trout removal because that is the typical lifespan of brook trout in southeast Minnesota. Trout were collected by electrofishing the entirety of each of the four stream reaches, with electrofishing gear appropriate for the stream size. In Coolridge and upper Hemmingway, we used a backpack electrofisher with one anode and dipnet. For lower Hemmingway, we used a tow barge with three anodes. Captured trout greater than 90 mm total length were measured and tagged with a passive integrated transponder (PIT) and given an adipose fin clip to allow monitoring of tag loss. After tagging, trout were released back into the pool from which they were captured. Brook trout were marked on eight occasions: September 2006, March 2007, August 2007, May 2009, October 2009, March 2011, September 2011, and March 2012. Trout were resampled every 3 months before brown trout removal and at 6-month intervals thereafter with one-pass electrofishing to calculate growth, survival, and movement. Trout were sampled more frequently in the pre-removal period as part of a study to examine seasonal differences in brook trout and brown trout demographics (Dieterman and Hoxmeier 2011; Hoxmeier and Dieterman 2013)

A barrier was constructed on the lower end of Coolridge Creek in June 2009. Brown trout were removed by electrofishing above the barrier starting in October 2009. We chose to remove brown trout in the fall when young of year were large enough to be efficiently captured, but before spawning occurred. Brown trout were removed from the entire stream length, with the highest densities occurring in the lower treatment reach. All brown trout captured by electrofishing were removed and stocked into Pine Creek, 2.5 km downstream from the confluence of Coolridge Creek. A subsample of brown trout (N = 303) were given adipose fin clips and stocked directly below the barrier in Coolridge Creek to monitor for barrier passage. Brown trout were removed during brook trout sampling every spring (March) and fall (September) for the next 3 years following the initial removal.

To estimate brook trout abundance and recruitment, we divided the total number of fish caught during a single pass by the length of stream sampled. We then expanded those numbers to calculate abundance by applying the capture probabilities from Program MARK (see below). We defined recruitment as abundance of age-0 fish collected in our fall sample. We used a paired BACI design to test for differences in abundance of age 0, adult, and large adult (>200 mm) brook trout before and after brown trout removal (Smith 2002). We did not include brook trout data from the first sample after brown trout removal (March 2010) in our analyses in order to allow time for treatment effects. The magnitude of brook trout response should be greater in lower Coolridge than in upper Coolridge because of the initial brown trout densities found in these reaches.

A subsample of brook trout was sacrificed for internal examination of gonads to assess maturity before and after brown trout removal during fall of 2008 and 2012. Maturation was determined by visual examination of gonads and scored as zero for immature and one for mature. We then used logistic regression with length as our dependent variable to calculate size-at-maturation for males and females. We developed 95 % confidence intervals using bootstrap methods. We resampled the dataset with replacement 10,000× to estimate the mean and used the 2.5 and 97.5th percentiles of the resulting distribution for lower and upper confidence limits (Efron and Tibshirani 1986).

Survival and movement

We estimated survival and movement while testing for effects of brown trout removal using a multistrata

Table 1 Habitat measurements for upper and lower reaches of Coolridge and Hemmingway creeks in southeast Minnesota

Stream	Reach	Length (m)	Wetted width (m)	Depth (cm)	Discharge (m^3/s)	Brown trout (N/km)		Summer water temperature (°C)	
						Pre	Post	Pre	Post
Coolridge	Upper	515	2.72 (0.27)	12.50 (0.91)	0.03 (0.00)	365.8 (162.9)	33.5 (10.2)	10.90 (0.05)	11.35 (0.05)
	Lower	1085	3.52 (0.16)	16.46 (0.91)	0.06 (0.01)	2025.8 (802.0)	472.9 (162.8)	11.71 (0.08)	12.57 (0.07)
Hemmingway	Upper	730	3.44 (0.16)	21.34 (3.05)	0.06 (0.02)	113.7 (31.8)	34.4 (7.4)	11.22 (0.07)	12.60 (0.07)
	Lower	935	4.17 (0.18)	37.20 (3.05)	0.11 (0.01)	1409.2 (118.8)	1316.3 (80.4)	13.28 (0.07)	14.19 (0.09)

Mean (±SE) wetted width, depth, and discharge taken during baseflow conditions. Mean brown trout abundance before and after experimental removal in Coolridge Creek. Summer water temperatures are daily means (±SE) from June through August before and after brown trout removal

Cormack–Jolly–Seber model in Program MARK (White and Burnham 1999). Multistrata models were analyzed for age-0 and adult brook trout to estimate apparent survival (*S*), capture probability (*p*), and movement (Ψ). Goodness of fit for the global model ($S_{(r\times t)}p_{(r\times t)}\Psi_{(r\times t)}$) was tested using a JollyMove (JMV) model structure in U-CARE (Choquet et al. 2009), with r denoting reach, t denoting time, and r × t their interaction. We relied on information from our previous work on brook trout demographics in this system to develop biologically meaningful models. Based on earlier work, capture probability is time dependent for adults and reach dependent for age-0 brook trout. We tested against the best model developed from Hoxmeier and Dieterman (2013) referred to as the pre-model (before brown trout removal). Our final candidate set of models included four models: time dependent, reach dependent, best pre model, and a test of the time by reach interaction (testing for brown trout removal effects). Models were ranked using AIC_c and were determined to be supported if they had a delta AIC (Δ_i) value less than two (Burnham and Anderson 2002). We also calculated Akaike weights (w_i) to examine the relative likelihood of each model. Because time between sampling was not the same for all occasions, we scaled all estimates in Program MARK to annual estimates.

Growth

We grouped brook trout into age-0, adults, and large adults (>200 mm) for comparison across reaches given that growth is size and age dependent. Growth in length for adults and large adults during spring and summer was calculated from individually marked fish captured on consecutive sampling occasions and expressed as growth rate (mm/day). Because we did not have recapture data for individually marked age-0 trout during the summer period, growth rates for those were calculated differently. We used length at capture for all age 0 trout collected in fall and divided that by the number of days since a standardized hatching date (April 1) to get a growth rate in mm/day. Growth rate data were logged prior to analyses to help normalize the data.

Relative condition factors (K_n; Le Cren 1951) were calculated for both brook trout and brown trout before and after brown trout removal. We combined across time periods and used lengths and weights of individual fish as our replicate for our before and after comparison. Differences in condition factor were tested using the interaction term in a two-way ANOVA of reach and time (before vs. after).

Results

Brown trout abundance in Coolridge Creek reached the highest level immediately prior to removal efforts. We removed 6052 (99.3 kg) brown trout from Coolridge Creek above the barrier in fall 2009. Follow-up sampling in spring 2010 removed another 520 brown trout from the stream. Total number of brown trout removed during subsequent sampling was less, but never reached zero. Mean abundance of age-0 brown trout significantly decreased in the upper treatment reach from 312 to 14/km after removal efforts (ANOVA; $P < 0.001$). Age-0 brown trout abundance also significantly decreased in the lower treatment reach from 1682 to 350/km ($P = 0.04$). Adult brown trout showed a significant decrease in our upper treatment reach (pre = 54/km, post = 20/km; $P = 0.01$), and decreased from 344 to 123/km in the lower treatment reach ($P < 0.001$). We only captured one brown trout above the barrier with an adipose clip indicating barrier passage. We were unable to remove all brown trout during the initial removal period which resulted in continued reproduction of brown trout in Coolridge Creek. After six removal attempts, brown trout still maintained successful reproduction in Coolridge Creek, although at lower levels.

Brook trout abundance increased in lower Coolridge Creek after brown trout suppression (2-way ANOVA interaction term, log-transformed; Age-0, $P = 0.02$; Adult, $P = 0.004$). The magnitude of response was greater in the lower reach than the upper reach of Coolridge Creek where few brown trout were present before removal efforts. In lower Coolridge Creek, adult brook trout increased from a pre-treatment mean of 42 to 161/km. Recruitment of age-0 brook trout was higher in lower Coolridge Creek after brown trout removal, increasing from a mean of 76 to 443/km. There was not a treatment effect in the upper reaches for age-0 brook trout (time × reach; $P = 0.86$), but there was a treatment effect for adult brook trout (time × reach; $P = 0.05$). Adult brook trout increased in upper Coolridge Creek from 104 to 206/km. Abundance of both adult and age-0 brook trout steadily

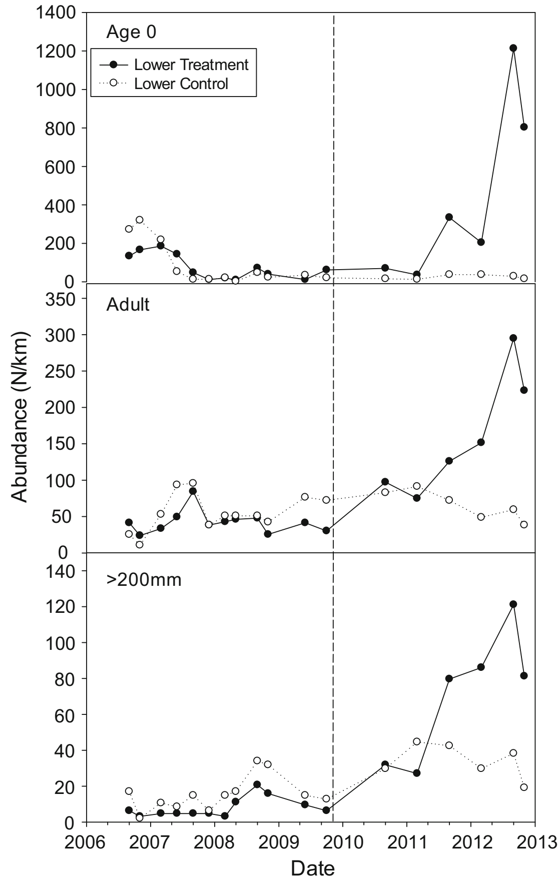

Fig. 3 Abundance of age-0, adult, and large adult (>200 mm) brook trout in *lower* Coolridge and Hemmingway Creeks from 2006 through 2012. *Dashed line* represents the beginning of *brown trout* removal in Coolridge Creek

increased after the initial brown trout removal, and reached their highest levels at the end of the study (Fig. 3). Brook trout in Coolridge Creek were more abundant in the lower reach (1508/km) compared to the upper reach (625/km) at the end of the study.

Survival

There was a reach-by-time interaction for survival and movement for both age-0 and adult brook trout that indicated an effect of brown trout removal (Table 2). Not all survival and movement parameters were estimatable in the interaction models. Therefore, to generate pre- and post-means and standard errors, we used estimates from models with time constrained to pre- and post-time periods for both adults and age-0 brook trout. Poor recruitment in Hemmingway Creek

Table 2 Ranking of multistrata Cormack–Jolly–Seber models estimating survival (S), capture probability (p), and movement (Ψ) for two age groups of brook trout

Model	AIC_c	Δ AIC_c	w_i	K	Deviance
Age-0					
S(r × t)p(r)Ψ(r × t)	**1156.12**	**0.00**	**1.00**	**39**	**382.43**
S(r)p(r)Ψ(r)	1182.81	26.69	0.00	12	435.46
S(.)p(r)Ψ(r)**	1192.14	36.02	0.00	9	484.29
S(t)p(r)Ψ(t)	1201.27	45.15	0.00	19	472.31
Adult					
S(r × t)p(t)Ψ(r × t)	**5084.38**	**0.00**	**1.00**	**116**	**1372.01**
S(t)p(t)Ψ(r)**	5187.50	103.12	0.00	39	1640.49
S(t)p(t)Ψ(t)	5219.26	134.89	0.00	50	1649.34
S(r)p(t)Ψ(r)	5291.02	206.64	0.00	26	1770.79

Subscripts denote time (t), reach (r), and their interaction (r × t). Corrected Akaike's Information Criterion (AIC_c), difference in AIC_c between the *i*th and the top-ranked model (Δ_i), Akaike weights (w_i), number of parameters (K), and model deviance are given. The most supported models ($\Delta_i < 2$) are highlighted in bold

** Best models from Hoxmeier and Dieterman (2013) before brown trout removal

made estimating survival and emigration of age-0 brook trout difficult in the post-treatment time period. In addition to low recruitment in Hemmingway Creek, suspected predation on brook trout by river otter *Lontra canadensis* in the upper reach resulted in high mortality during winter 2010–2011. Survival of age-0 brook trout increased in both reaches on Coolridge Creek after brown trout removal, whereas survival decreased in both control reaches (Table 3). Survival also increased for adult brook trout in Coolridge Creek after brown trout removal, but also increased in our lower control reach, suggesting no benefit of brown trout removal on adult brook trout survival.

Movement

A lower percentage of adult brook trout moved out of lower Coolridge Creek after brown trout removal (Table 3). Movement of brook trout from the upper portion of Coolridge Creek into the lower portion where brown trout were removed increased after the removal (Fig. 4). For age-0 brook trout, movement out of lower Coolridge was similar before and after brown trout removal.

Growth

Growth of both age-0 and adult brook trout increased in lower Coolridge Creek after brown trout removal relative to growth in the lower control stream (time × reach; $P < 0.001$; Fig. 5). There was not a treatment effect on growth rates of large adults (>200 mm) in either reach (time × reach; $P > 0.29$). The number of large adults per kilometer increased in lower Coolridge Creek relative to lower Hemmingway Creek after brown trout removal (time × reach; $P = 0.004$; Fig. 3). Brown trout removal had no effect on brook trout condition in either the lower (pre = 1.15, post = 1.16; time × reach; $P = 0.32$) or upper reaches (pre = 1.18, post = 1.17; time × reach; $P > 0.44$). There also was no treatment effect on brown trout condition (time × reach; $P = 0.10$).

Maturation

Both males and females matured at a small size in Coolridge Creek regardless of brown trout abundance. There was no difference in length at maturity before and after brown trout removal in Coolridge Creek. Male brook trout matured at 118 mm before brown trout were removed and at 112 mm after removal (Fig. 6). We did not collect any immature individuals in Hemmingway Creek during the pre-treatment time period, so we were unable to calculate size at maturity during that time. Post-treatment male brook trout were slightly larger at first maturity in Hemmingway Creek than in Coolridge Creek.

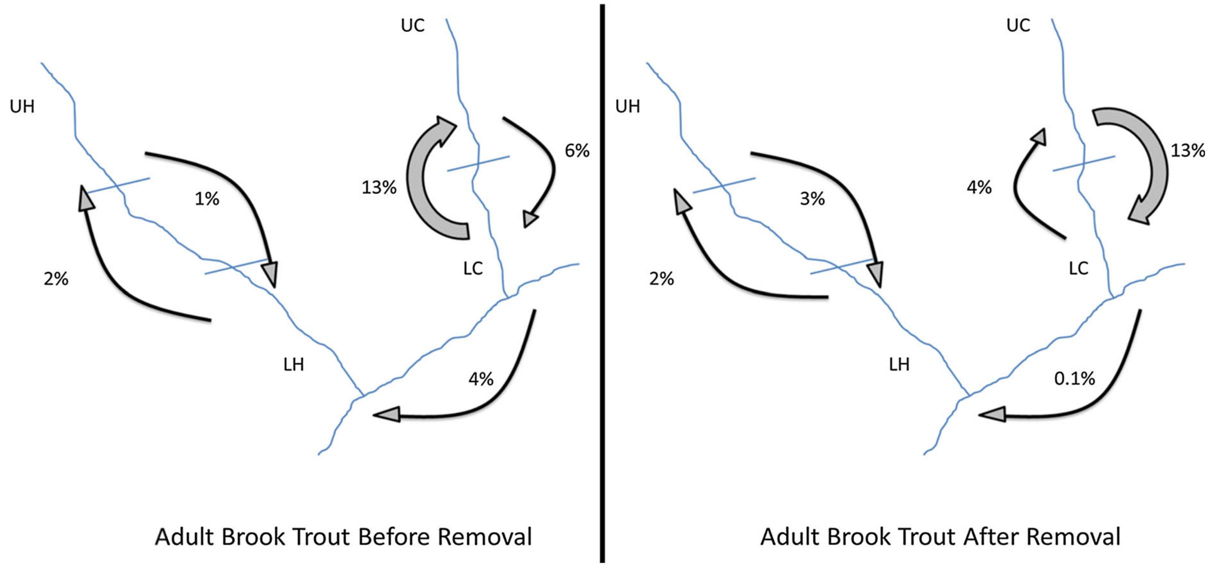

Fig. 4 Annual movement rates of adult brook trout before and after brown trout removal in Coolridge Creek. *Upper* Coolridge (UC) and *upper* Hemmingway (UH) were dominated by *brook trout* and had low *brown trout* density, whereas *lower* Hemmingway (LH) and *lower* Coolridge (LC; prior to removal efforts) had high *brown trout* density

Discussion

We identified forced emigration and decreased recruitment as primary mechanisms controlling abundance of brook trout in the presence of brown trout. Brook trout abundance increased after brown trout removal despite an increase in stream temperature. Brook trout size structure also increased as a result of increased growth and decreased emigration of large fish. Adult brook trout survival was not affected by brown trout and may not be a good metric for measuring the effects of a non-native trout species. In fact there is little evidence for competition among adult trout in the literature when using survival as a comparative metric. For example, adult cutthroat trout survival remained the same after removal of either brook trout or brown trout (Peterson et al. 2004; McHugh and Budy 2006). In our case, adult survival may have been driven more by flood events rather than by competitive interactions (Hoxmeier and Dieterman 2013).

The use of adult survival to measure the effects of an invasive species on a native trout population could be misleading in suggesting that there are no negative effects. For example, McHugh and Budy (2006) did not find any evidence of decreased adult survival of cutthroat trout in the presence of brown trout, but they did find that movement was affected. The nearly doubling of survival in our study cannot be attributed to brown trout removal given that the same magnitude of effect was observed in our control reach. Lack of a control in this study would have led to an incorrect conclusion about the effects of brown trout on brook trout survival. Similarly, if movement had not been accounted for, emigration out of the study reach prior to removal would have been interpreted as decreased survival attributable to brown trout competition. Also, not allowing a fish to emigrate may lead to decreased survival if that fish does not have access to resources that it needs. Most likely, a fish will move until it finds the resources that it needs, or die in the process if none are found. Because adult survival nearly doubled in our control reach, an increase in abundance could have been expected. However, brook trout abundance remained the same in the control reach despite the increase in survival due to low recruitment and a lack of immigration.

While adult brook trout survival in this system may be primarily dependent on abiotic factors, age-0 survival and reproductive success appears to be influenced by the presence of brown trout. We did not measure age-0 recruitment until their first fall, but little dispersal of brook trout from spawning locations would be expected before then (Hudy et al. 2010; Kanno et al. 2011), thus we surmise that spawning

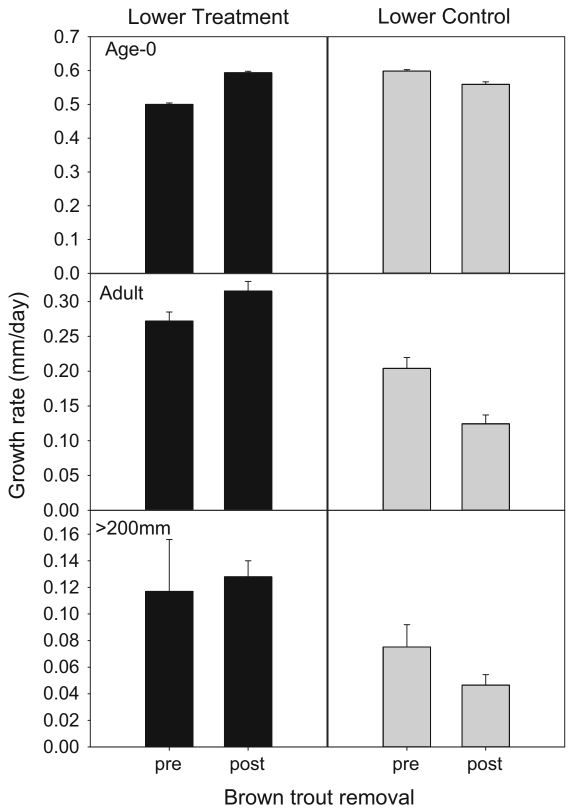

Fig. 5 Mean (±SE) daily growth rates of age-0, adult, and large adult (>200 mm) brook trout in lower Hemmingway (control) and *lower* Coolridge (treatment) creeks before and after *brown trout* removal

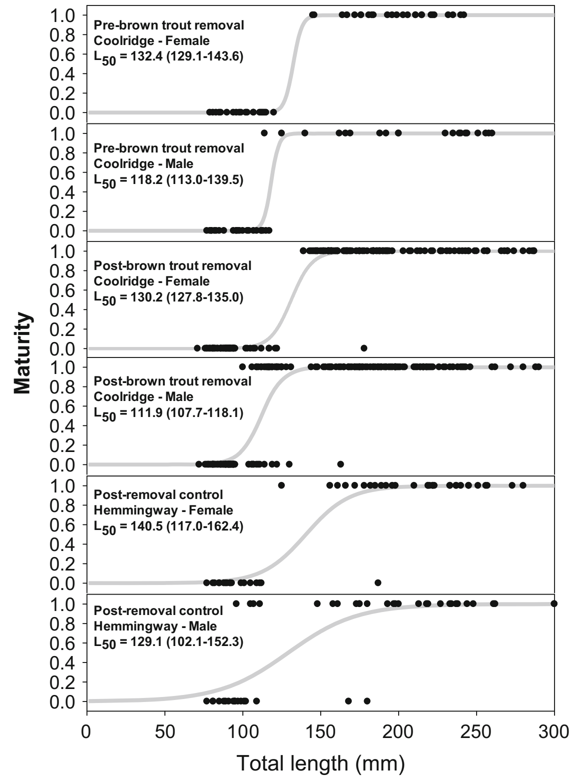

Fig. 6 Size at maturity (95 % CI) for brook trout collected in Hemmingway (control) and Coolridge (treatment) creeks before and after *brown trout* removal

success and age-0 trout survival was high in the treatment reach after brown trout removal. Intense competition often occurs during the larval stage due to high densities that occur during this period, but density-independent factors often limit juvenile and adult salmonid populations once densities are reduced (Hearn 1987). However, previous studies have documented few if any interactions between age-0 brook trout and brown trout. For example, brown and brook trout had similar first-year growth rates in Egypt Creek, Michigan, suggesting minimal competition (Fausch 1981). Rather, age-0 survival may have increased due to decreased predation pressure from adult brown trout. Large brown trout have been shown to reduce brook trout populations by preying on juvenile brook trout (Alexander 1977). Increases in age-0 brook trout abundance after brown trout reduction may also have been the result of increased spawning success. Brook trout reproduction has been shown to be negatively influenced by brown trout in small streams (Grant et al. 2002; Sorensen et al. 1995). Likewise, McGrath and Lewis (2007) suggested that non-native brook trout negatively affected recruitment of native cutthroat trout. Although it's unclear as to what if any time period was critical for survival of brook trout during their first year of life (egg, larval, juvenile), our results suggest that recruitment to the first fall was negatively influenced by brown trout.

Our results are consistent with previous studies documenting an increase in native trout abundance following suppression of a non-native trout species (Moore et al. 1983; Peterson et al. 2004). Brook trout abundance steadily increased throughout the 3-year time period after brown trout removal. Density of brook trout at the end of the study was similar to that of pre-treatment brown trout, and brook trout may have reached carrying capacity. Often, invasive trout populations reach levels above that of the native species it replaces (Benjamin and Baxter 2012). Likewise, when invasive species are removed, native species do not

Table 3 Annual survival and emigration estimates (SE) of brook trout for before (pre) and after (post) brown trout removal in Coolridge Creek

Reach	Survival (%)		Emigration (%)	
	Pre	Post	Pre	Post
Age 0				
UC	12.0 (8.0)	77.0 (13.9)	13.5 (7.7)	5.1 (2.7)
LC	20.7 (14.1)	31.8 (10.0)	13.5 (9.2)	16.0 (7.6)
UH	30.9 (9.0)	0.5 (0.9)	3.7 (2.1)	0.0 (0.0)
LH	17.7 (6.8)	7.0 (11.8)	0.9 (0.9)	0.0 (0.0)
Adult				
UC	21.3 (3.0)	40.0 (3.7)	5.6 (1.5)	12.9 (2.3)
LC	23.1 (3.8)	48.7 (3.9)	12.9 (2.7)	3.8 (1.2)
UH	41.1 (3.5)	26.1 (3.6)	0.9 (0.5)	3.1 (1.5)
LH	24.4 (3.5)	44.4 (4.8)	1.8 (0.9)	1.9 (1.3)

Parameter estimates were generated in Program MARK by constraining the data based on pre and post time periods. Reaches were defined by initial brown trout density. Lower Coolridge (LC) and lower Hemmingway (LH) had high brown trout density whereas upper Hemmingway (UH) and upper Coolridge (UC) had low brown trout densities

reach levels of the previous invasive fish. For example, brown trout production in Valley Creek, Minnesota was nearly double that of pre-invasion brook trout production (Waters 1999). We expect that brook trout biomass in Coolridge Creek would likely be maintained at a level slightly below previous brown trout biomass.

In addition to an overall increase in abundance, the number of larger brook trout also increased relative to the size of the population. Larger brook trout in the treatment area resulted from larger brook trout moving into the area and also faster growth of residents. Growth of native trout species is often lower in sympatry than in allopatric populations (McHugh and Budy 2006; Seiler and Keeley 2009) and diet overlap between brook trout and brown trout in Minnesota streams is high (84.6 %; Zimmerman and Vondracek 2007). Increased growth of brook trout in our study likely resulted from a competitive release from brown trout given that brown trout often outcompete brook trout for both feeding and resting areas (Fausch and White 1981; Blanchet et al. 2007). Also, the treatment reach had better growth potential for brook trout given the increased water temperatures and feeding areas compared to the upper reach where brook trout were previously isolated. Total length of age-0 brown trout in the fall increased in Coolridge Creek during the post-treatment period, similar to that of age-0 brook trout suggesting the influence of density-dependent growth mechanisms. While density-dependent growth plays a role, removal of brown trout ultimately increases availability of prey for brook trout through increased feeding opportunities.

The lack of an effect on brook trout condition after brown trout removal is similar to results of previous studies. Cutthroat trout did not show an increase in condition after removal of brook trout in Wyoming (Novinger and Rahel 2003). Similarly, there was no difference in condition of greenback cutthroat trout *O. clarkii stomias* in allopatry versus sympatry with brook trout (McGrath and Lewis 2007). Condition of cutthroat trout did decrease in the presence of brown trout when they were held in enclosures, but not at a population level in unconfined stream reaches (McHugh and Budy 2005, 2006). Body condition may only be affected if the native species is not allowed to emigrate into more favorable areas with less interspecific competition.

Habitat differences can result from innate habitat preferences or through interactive segregation. Brook trout dominated the headwaters of both streams suggesting that they are better adapted to these reaches (Magoulick and Wilzbach 1998). However, after brown trout removal, brook trout occupied the lower reach of Coolridge Creek at higher densities than found in the upper reach. Also, growth of brook trout was faster in the downstream reach than in the upstream reach. Our results suggest brook trout were displaced into the headwater reach through interactions with brown trout. Emigration of a subordinate species is not well documented in salmonids; however, movement of the subordinate trout species has been shown to be limited in sympatric populations (McHugh and Budy 2006). The current study confirms previous work that suggests forced emigration is an important factor influencing longitudinal trout distribution (Hoxmeier and Dieterman 2013).

Brook trout are known to display phenotypic plasticity in size and age of maturation in response to environmental changes (Hutchings 1996). In this case, brook trout could be maturing at a small size because of competition pressures from brown trout. However, even after removal of brown trout, brook trout continued to mature at a small size. Size at maturation may not respond as quickly to brown trout removal as recruitment and growth. It may take brook trout longer to delay maturation in this system, especially if other stressors are still acting on the population (e.g., flooding).

Nonnative trout removals are a common management technique in the Western and Southeastern United States; however, success of nonnative trout removals has varied either in terms of removing the nonnative species or the resultant effect on the native species after removal (Moore et al. 1983; Kulp and Moore 2000; Meyer et al. 2006). Our study adds to the growing literature that demonstrates the difficulty of completely eradicating non-native trout from streams (Meronek et al. 1996; Thompson and Rahel 1996; Meyer et al. 2006). We were unable to remove all adult brown trout from Coolridge Creek due to areas that were difficult to electrofish because of large woody debris and deep pools. As a result, enough brown trout remained in Coolridge Creek to have successful spawning each year. However, our program was able to successfully suppress brown trout abundance during the 3 years following initial removal and resulted in increased abundance of native brook trout.

Conclusions

Brook trout abundance and size structure in the lower portion of Coolridge Creek increased when brown trout were suppressed, suggesting that habitat was not limiting brook trout distribution in this system. The largest contributors to increased brook trout abundance after brown trout removal included increased recruitment and immigration into the lower treatment reach. Comparing adult survival at the population level or condition at the individual level may not reveal negative consequences on native species from an invader. Successful brook trout management needs to address both biotic and abiotic factors. Any attempts to conserve brook trout populations through watershed (decrease flooding magnitude) or instream (habitat improvement) management practices will only be effective if brown trout are also controlled.

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