SEASONAL MOVEMENT, GROWTH, AND MORTALITY OF BROOK TROUT IN SYMPATRY WITH BROWN TROUT IN HEADWATER STREAMS IN SOUTHEAST MINNESOTA[1].

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Abstract: Although laboratory studies have provided evidence for competition between brook trout and brown trout, it is unknown how this competition affects larger scale demographics in a natural setting. We examined seasonal demographics of Driftless Area brook trout populations in the presence of high and low brown trout densities. Seasonal and spatial patterns in growth, recruitment, survival and movement of brook trout were monitored in two southeastern Minnesota streams divided into upper and lower reaches based on the abundance of brown trout. We estimated survival and movement while testing for effects of stream reach and season using a multistrata Cormack-Jolly-Seber model in Program MARK. Multistrata models were analyzed for three age groups (age-0, age-1, and age-2+) to estimate apparent survival, capture probability, and movement. Survival was dependent on season rather than study reach and was lower during flood events. Age-0 brook trout emigrated from upper reaches to lower reaches, whereas, adult brook trout emigrated out of the downstream brown trout dominated reaches. Growth in spring and summer did not differ across streams or treatments for the youngest age classes. For age-2+ brook trout, however, growth was higher in areas where brown trout were less abundant. Competition can be age or size dependent; our results show evidence for adult interactions, but not age-0. Our results suggest that brown trout may be influencing adult brook trout distribution through forced emigration. Also, decreased growth rates of adult brook trout in the presence of brown trout warrants further research on possible mechanisms.

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Although competition among salmonids has been well studied in both laboratory and field studies (see review by Hearn 1987), it is still unclear where and when these interactions take place. Much attention in terms of replacement of native trout species is focused in the western US where native cutthroat trout (*Oncorhynchus clarkii*) have been replaced by both brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). While it is understood that brook trout negatively affect cutthroat trout in their native range, it's been only recently that we've gained a better understanding of when and where these interactions take place (Dunham et al. 2002). For example, it appears that brown and brook trout have a competitive advantage over cutthroat trout at lower elevations in many mountainous streams (Budy et al. 2008). Competition usually does not occur throughout the year, but rather during a critical time period, for example, when prey or spawning habitat is limiting. In addition to seasonal and reach effects, age groups can also be affected differently. 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).

A paradox among salmonids is that while brook trout are considered invaders in Western US and in Europe, they have difficulty sustaining populations in their native range due to competition from non-native salmonids (Fausch 2008). Brook trout in Minnesota are at the western edge of their native range and therefore have added importance in terms of conservation (Lesica and Allendorf 1995; Haak et al. 2010). In the Midwestern United States, native brook trout are typically found in lower abundance than introduced brown trout. Much of this has to do with the successful management of brown trout by fisheries management agencies. Because of degraded stream conditions brown trout were favored over brook trout by fisheries agencies given their higher probability for success. Recent improvements in watershed and riparian areas in many parts of the Midwest has made brook trout management a viable option once again, however, increasing numbers of brown trout have 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 competition or inherent longitudinal habitat differences is unclear (Magoulick and Wilzbach 1998b). Differences in trout distribution have been attributed to water temperature, elevation, gradient, and stream size (Kozel and Hubert 1989; Taniguchi et al. 1998; Bozek and Hubert 1992). Water temperature may play a role in this distribution by mediating competition between creek chubs (*Semotilus atromaculatus*) and trout, but it did not explain distribution patterns between brook trout and brown trout (Taniguchi et al. 1998). However, brook trout were more aggressive than brown trout in colder water temperatures in a laboratory setting (Magoulick and Wilzbach 1998a). Another potential reason brook trout do better in headwater areas is that their life history is suited to the stream conditions. Pools are generally smaller and water temperatures colder, which may benefit a species such as brook trout with limited growth potential and early maturation (Öhlund et al. 2008).

Streams located in the Driftless Area of Minnesota, Wisconsin, Iowa, and Illinois offer a unique setting to study salmonid interactions. The Driftless area, so called because it was missed by the last Wisconsin glaciation period, is characterized by limestone karst topography that creates numerous sinkholes and groundwater springs. Coldwater trout streams either originate from these groundwater springs or are created as these springs provide input along the course of the stream. Stream water temperatures warm (summer) or cool (winter) as they become further away from spring inputs. These streams lack the drastic elevation changes of trout streams in the Appalachians or Rocky mountains. These streams are also high in alkalinity and highly productive (Kwak and Waters 1997). In addition to brook trout, brown trout have naturally reproducing populations in most coldwater streams in southeastern Minnesota. Rainbow trout (*Oncorhynchus mykiss*) are stocked in some southeast Minnesota streams, but do not naturally reproduce.

Evidence of interspecific competition can be obtained in a field setting by examining measures of survival, recruitment, and growth between areas with different densities of a presumed competitor. While this approach lacks the control inherent in a laboratory setting, the technique provides a better description of whole populations under natural conditions. It also allows for emigration of the subordinate species, a result often not obtainable in closed studies. Gathering basic demography data on brook trout is also important because very little information of this type exists for the Driftless Area. In addition, better understanding competitive interactions, insight on seasonal recruitment, growth, movement, and mortality is the basis for any type of conservation plan for native species.

The objectives of our study were to describe seasonal demographics of a unique brook trout population in the presence of high and low brown trout densities. Specifically, we quantified seasonal and spatial patterns in growth, recruitment, survival and movement of Driftless Area brook trout in two southeastern Minnesota streams divided into upper and lower reaches based on the abundance of brown trout.

Methods

Study Area

To examine spatial differences in growth, movement, and survival, we chose three interconnected coldwater streams in Southeast Minnesota (Figure 1). All three streams had naturally reproducing brook trout and brown trout present in varying densities. Brook trout populations in these three streams were genetically unique to southeastern Minnesota (Hoxmeier et al., in prep). Hemmingway Creek is 2.9km in length and flows into Pine Creek, a larger 4th order stream that is 28km in length. Coolridge Creek is a small stream 1.7km in length that also flows into Pine Creek, 0.4km below the mouth of Hemmingway Creek. Watersheds of these three streams are primarily a mix of hardwood forests, pasture, and row crop agriculture. To test for brown trout density effects, we divided Hemmingway and Coolridge creeks into two reaches based on brown trout density. The downstream ends of both Hemmingway and Coolridge Creeks had brown trout densities 3 to 28 times higher than the upstream portions. Therefore we set up our treatments as upper Hemmingway (UH, 730m) and upper Coolridge (UC, 515m) as brook trout dominated with low brown trout density, and lower Hemmingway (LH, 935m) and lower Coolridge (LC, 1085m) as few brook trout and high brown trout density (Figure 1). We did not have landowner permission to access the middle portion of Hemmingway Creek. Pine Creek had very few brook trout and high brown trout density and served as a corridor for fish travel between Hemmingway and Coolridge. We did not find many brook trout from Coolridge or Hemmingway that moved and stayed in Pine Creek and therefore, we did not include Pine Creek in any analyses.

Fish sampling

Trout were collected by electrofishing the entirety of each of the four stream segments beginning in September 2006. Electrofishing gear was dependent on the size of the streams. For lower Hemmingway, we used a tow barge with three anodes. In lower and upper Coolridge, and upper Hemmingway, we used a backpack electrofisher with one anode and dipnet. Captured trout greater than 100mm total length were measured and tagged with a passive integrated transponder (PIT) and given an adipose fin clip to monitor any tag loss in future sampling occasions. Tags were initially inserted into the body cavity, but after observing tag loss, we began inserting tags into the dorsal musculature (Dieterman and Hoxmeier 2009). After tagging, trout were released back into the pool from which they were captured. Brook trout were marked on three occasions: September 2006, March 2007, and August 2007. Trout were resampled approximately every three months to calculate seasonal survival, movement, and growth estimates: spring, summer, fall, and winter. We typically sampled in the months of March, May, August, and November.

To confirm brown trout density treatments and estimate brook trout recruitment, two pass depletion population estimates were conducted in randomly chosen pools in each stream reach in the spring and fall. We defined recruitment by abundance of age-0 fish collected in our fall sample.

Brook trout were divided into three age groups based on length frequency histograms and known age fish. Known age fish were those tagged at age-0 and followed though to older ages. Our age groups consisted of age-0, age-1, and age-2+ (those fish age-2 and older; Figure 2 and 3). These age groups were chosen based on ecologically important life stages. Age-0 brook trout typically use different stream habitats than adult brook trout and are sexually immature until their first fall. Our age-1 group consisted of sexually mature males and females, and a transition period in terms of habitat use. The age-2+ group is where most brook trout become vulnerable to angler harvest. Because age-0 brook trout were not vulnerable to our collection methods until fall, we could not calculate estimates of growth, survival, and movement for spring and summer.

Growth in length was calculated from recaptured fish and expressed as growth rate (mm/day). We only used fish captured in consecutive sampling occasions for measurements of seasonal growth. Because we were interested in examining reach effects on growth, fish that moved throughout reaches between sampling occasions were not included in growth analysis. Also, given that growth is size dependent, we used size groups of <150, 150-200, and >200mm for comparison across reaches. These size groups correspond to age-0, age-1, and age-2+ in the fall, but they do not correspond to these age groups throughout the year.

Survival and movement

We estimated survival and movement while testing for effects of stream reach and season using a multi-strata Cormack-Jolly-Seber model in Program MARK. Multistrata models were analyzed for each age group to estimate apparent survival (*S*), capture probability (*p*), and movement (*Ψ*). Effects of season (t) and stream reach (r) were tested for each parameter. Before developing a candidate set of models, goodness of fit for the global model ($S_{(r*t)}p_{(r*t)}\Psi_{(r*t)}$) was tested using a Jolly-Move (JMV) model structure in U-CARE (Choquet et al. 2009). A good fit to this model would mean that estimates of survival, movement, and capture probability are not being influenced by certain groups of tagged fish behaving differently. For example, a group of tagged fish may be trap dependent in one reach but not the other, thus biasing survival estimates. We then proceeded to develop demographic models for brook trout following the suggestions of Lebreton et al. (1992), in that we initially held both survival and movement constant to find the best capture probability based on lowest bias-corrected Akaike's Information Criteria scores (AIC_c). We then used this capture probability model while holding survival constant to find the best movement model. Finally, using this "best" model for capture probability and movement, we developed a candidate set of models for survival. Estimates of survival are considered apparent survival because fish could have moved out of our study area. Our candidate set of models included 6 models: global model with all three parameters varying by reach and season, survival varying by season, by reach, reach and season, constant, brown trout density, and brown trout density and season. Brown trout density (treatment) was tested for by grouping both upper stations (UH and UC) for a low brown trout density treatment, and both lower stations (LH and LC) representing high brown trout density using the Parameter Information Matrix (PIM) chart function in Program Mark. 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. If more than one model had support we used model averaging to estimate parameter values. Because time between sampling was not exactly three months for all occasions, we scaled all estimates in program MARK to three month intervals.

Because tag retention for brook trout tagged in the body cavity was not 100%, we removed the appropriate number of fish never re-captured again to account for tag loss. We assumed tag loss was immediate, and therefore we randomly deleted 16% (based on tag loss estimates) of capture histories for fish that were tagged in the body cavity and never recaptured again.

Habitat measurements

To help explain spatial patterns in brook trout demographics, we measured select habitat features in each reach. Habitat measurements were taken at the beginning and end of the study during baseflow conditions. Habitat measurements were taken at 2 locations in Pine Creek, seven locations in Hemmingway Creek, and nine in Coolridge Creek. Wetted width measurements were taken at the mid-point of each pool and riffle and averaged for the entire reach. Depth measurements were taken at the midpoint of each pool and riffle in the thalwag and at half the distance from the thalwag to shore (three measurements at each transect). Slope was measured from longitudinal elevation data collected using a laser transit. Streambed substrate was measured at 100 points along the stream reach and classified according to Rosgen (1996). The number of habitat sampling locations was based on perceived changes in stream characteristics. Individual pools were numbered and marked the length of each stream. Cover for trout was defined as instream rock, instream vegetation, overhead bank, wood, and water depths greater than 1m. Each of these cover types were measured in terms of length and width. This was used along with wetted widths and stream length to get percent total cover. Discharge measurements were taken at baseflow with a Marsh-McBirney electromagnetic flow meter. To get a regional daily discharge pattern, we used the closest monitoring gage in the watershed, located 34km downstream in the Root River, a 6th order stream.

Because temperature could potentially affect movement and survival, continuous temperature loggers were placed in each stream segment and recorded water temperature every half hour. Also, because we had access to the entire reach of Coolridge Creek, we collected longitudinal temperature data with a handheld YSI temperature meter during July 2008 to characterize potential temperature differences along the stream course.

Results

Fish sampling

Trout were sampled on 10 occasions from September 2006 thru October 2008. In both Hemmingway and Coolridge creeks, density of brown trout was higher in the lower portions of the streams and was reduced near the headwaters (Table 1). The headwaters portions of both streams typically had higher densities of brook trout than lower reaches across all years (Table 1). This distributional pattern was also evident during our single pass electrofishing collections in the spring summer and winter. Combining across all sampling occasions, the percent of trout comprised of brook trout increased upstream. Brook trout only represented 0-31% of the trout population in the lower pools whereas, in the uppermost pools, brook trout were the only trout sampled (Figure 4). Slimy sculpin (*Cottus cognatus*) and mottled sculpin (*Cottus bairdi*) were also present in all stream segments. We marked 286 individual brook trout in September 2006, another 155 in March 2007, and an additional 168 in August 2007. Of the 609 brook trout marked, we recaptured 284 individuals at least once during subsequent sampling occasions. Eighty-five fish that were tagged and never recaptured were removed prior to MARK analyses to account for tag loss (Table 2).

Age-0 brook trout recruitment was highest in 2006 followed by two relatively poor year-classes in 2007 and 2008 (Table 1). Age-0 brook trout abundance was highest in upper Coolridge in 2006 and 2007, but no other patterns were evident. Recruitment patterns for brown trout were similar to brook trout in that 2006 was a strong year-class and 2007 was poor. However, in 2008 brook trout did not produce a strong year-class, whereas brown trout recruitment was high.

Growth

Seasonal growth patterns were apparent across all study reaches, with fastest growth rates occurring in spring and summer (Figure 5). Growth in spring and summer did not differ across streams or treatments for the youngest age classes (Figure 6.). For age-2+ brook trout, however, growth was higher in upstream areas with low brown trout abundance. Stream differences were also apparent with Coolridge having higher growth rates than Hemmingway (Figure 5 and 6). Although some growth differences across reaches and streams were evident, differences in growth among individuals was large (Figure 7).

Survival and movement

Global models for all three age groups were a good fit to the data based on a JollyMove (JMV) model structure tested in U-CARE ($P > 0.30$ for all three models). Therefore, we proceeded to develop candidate sets of models described in the methods.

Our best model for age-0 brook trout was constant survival with capture probability and movement varying by reach (Table 3). However, a model with survival varying by treatment also deserved consideration. These two models combined for 90% support related to model weights. We generated parameter estimates by model averaging these top two models. Survival estimates were similar between reaches with high brown trout density (69%) and low brown trout density (71%). These estimates apply equally to both fall and winter. We could not estimate annual survival of age-0 because we did not have spring and summer estimates of survival. Nor could we calculate any estimates in 2007, given poor recruitment in that year. Age-0 brook trout had higher emigration rates from upper reaches than from lower reaches in both streams (i.e., net downstream movement) (Table 4). Emigration rates were lower from Hemmingway Creek than Coolridge Creek. There was also movement of brook trout out of lower Coolridge and into lower Hemmingway (Figure 8). Capture probabilities ranged from 0.35 to 0.64 for age-0 brook trout depending on reach of capture (Table 4). Lower Hemmingway had the poorest capture probability, which may have resulted from the large pool areas found in this reach.

The best model for age-1 had capture probability and survival both being season dependent with movement dependent on reach (Table 3). This model had about 100% support based on w_i. Three-month survival estimates ranged from 41 to 100%, with the lowest survival periods in winter 2006 (53%) and summer 2007 (41%; Figure 9). We could not generate estimates of movement and survival for age-1 brook trout in 2008 because there were too few individual in this cohort. Seasonal survival estimates were multiplied across one year (winter 2006 thru winter 2007) to generate an annual survival estimate of 9% for age-1 brook trout. Movement of age-1 brook trout showed the opposite trend of age-0, with a higher percentage moving upstream than downstream (Figure 8). Movement rates were lower in Hemmingway than Coolridge Creek. While movement of age-1 brook trout from Coolridge to Hemmingway was still recorded (1%), it was much less than that observed for age-0. Season affected capture probabilities for age-1 brook trout, with the most efficient captures in both winter events (2006, 0.78; 2007, 0.72). We were least efficient at capturing age-1 brook trout in the fall (2006, 0.38; 2007, 0.55).

Age-2+ fish showed similar results to age-1, in that survival was dependent on season and movement was dependent on reach (Table 3). This model was strongly supported over the other candidate models (w_i = 98%). Three-month survival estimates followed the same trend as age-1 estimates, with survival being lowest in winter 2006 (45%) and summer 2007 (51%; Figure 9). Survival for age-2+ brook trout was generally higher than for age-1 brook trout, but standard errors overlapped. Annual survival from winter 2006 thru winter 2007 was 13% for age-2+ brook trout. The only movement for age-2+ brook trout was between UC and LC, with a higher percentage of fish moving upstream in each season (Figure 8). Age-2+ capture probabilities were not affected by either season or stream reach, but remained constant at 60 percent.

Because movement was not dependent on season, we combined our 3-month emigration estimates into an annual estimate. While movement rates were low for an individual season, on an annual basis they become more substantial. The most movement occurred within Coolridge Creek for all three age classes. Forty percent of age-2+ brook trout emigrated from LC to UC annually. In terms of monitoring site fidelity, of the 284 individuals recaptured at least once, 56% did not move. We considered a brook trout sedentary if it was captured within three pools of the original capture pool.

Habitat

Spatial patterns in habitat were evident, with the upper reaches of both streams being narrower, shallower, and having less discharge than their corresponding lower reaches (Table 5). Lower Hemmingway was the deepest reach and provided the most cover for adult trout. Lower Coolridge and Upper Hemmingway were similar to each other geomorphically, however, UH had more adult trout cover. Upper Coolridge was the smallest reach in terms of area, and it also had the least amount of discharge. Percent fines were less in upper reaches of both streams which may have resulted from higher gradients. Hemmingway Creek had more adult trout cover than Coolridge Creek. Coolridge habitat changed frequently due to flooding and an unstable stream channel.

Three flooding events took place during our study period that would have affected our winter 2006, summer 2007, and summer 2008 estimates. The flooding that occurred in summer 2007 was the highest event ever recorded in southeastern Minnesota (Figure 10).

Temperature loggers were only recovered from 3 reaches in 2008 because flooding dislodged temperature loggers located in LC. We replaced temperature loggers in these reaches after the study to try and capture the temperature differences among reaches. We recovered temperature loggers in 3 reaches again in 2009. Both UC and UH experienced less variation in seasonal temperatures than did the lower reaches given their proximity to groundwater inputs. Mean July water temperatures were higher in the lower reaches compared to the upper reaches (Table 5). A longitudinal temperature profile was taken in July 2008 in Coolridge Creek. We specifically chose to sample during a time of higher than average air temperature to try and capture the range of variability in stream temperature. The longitudinal profile confirmed temperature logger data, showing a gradual temperature change from 11.9 °C in the headwaters to16.6 °C in the lowest portion (Figure 11).

Discussion

Brook trout demographics differed between study reaches with high and low brown trout density, especially in terms of growth and movement. While we did not see any evidence for competitive interactions in survival and recruitment, this may have been outweighed by environmental factors. Older age classes appeared to have been affected more by abundant brown trout than age-0 brook trout. Juvenile brook trout (68 – 72.5 mm FL) were the dominant competitor over equal sized brown trout in a laboratory study (Fausch 1981), while larger brown trout (>150mm) excluded equal sized brook trout from resting positions but not feeding positions (Fausch and White 1981). Conversely, brook trout competed with cutthroat trout at age-0 and age-1, but older cutthroat trout were not affected (Peterson et al. 2004). In contrast to our field results, age-0 brown trout displaced age-0 brook trout into unfavorable areas of the water column in a lab setting (Blanchet et al. 2007).

Growth

Growth of native trout can be reduced when in sympatry with a competing salmonid (Seiler and Keeley 2009). For example, growth of cutthroat trout was reduced in the presence of brown trout in Utah (McHugh and Budy 2006). We found higher growth rates for age-2+ brook trout in the upper reaches of both streams, where brown trout density was low. Conversely, brown trout have been shown to grow faster than brook trout in sympatry during the spring (Carlson et al. 2007). In laboratory conditions, brook trout lost weight in the presence of brown trout (Dewald and Wilzbach 1992). We did not find differences in growth rates of age-0 trout. Similarly, brown and brook trout had similar first year growth rates in Egypt Creek, Michigan (Fausch 1981).

Water temperatures and trout density could also play a role in brook trout growth observed in our study. Water temperatures were similar between UH and LC as were growth rates between these two reaches. Growth was slowest in LH where water temperatures were warmest, especially for age-2+ trout. High summer water temperatures in a Michigan stream had negative effects on brook trout growth for age -2 fish but not younger age classes (Drake and Taylor 1996). Whereas, faster growth was associated with warmer water temperatures and increased flows in the summer for brook trout in Massachusetts (Xu et al 2010a). Water temperatures in our study never reached a thermal maximum where brook trout would be stressed. Baldwin (1956) showed brook trout growth to be highest at 13 C with good growth occurring between 9 and 17 C. Overall trout density was higher in the lower portions of the streams than in the upper portions and could also explain the slower growth. Brook trout can experience density dependent growth during stressful times when water temperatures are high (Utz and Hartman 2009; Xu et al. 2010a). Southeastern Minnesota streams are very productive given their high nutrient content and are usually not prey limited (Kwak and Waters 1997); hence we would not have expected to see density dependent growth for brook trout in this study. Instead it is more likely that growth differences we observed were caused by potential interference competition from brown trout.

Brook trout grew fastest in spring and summer, as noted in previous studies (Carlson et al. 2007; Utz and Hartman 2009; Xu et al 2010a), and growth was almost non-existent in winter (Cooper 1953). High flows coupled with low water temperatures produced slow growth rates of brook trout in Massachusetts (Xu et al. 2010b). While some growth was explained by reach and season, there was substantial individual variation, as seen previously with brook trout (Cooper 1953). Differences among individuals could be a result of some fish being able to select preferred feeding areas within their respective reaches. Another reason could be onset of maturity. Many of the brook trout in southeastern Minnesota sexually mature at age-0; however, a delay in maturation may allow those fish to experience higher growth rates (Hoxmeier et al., in prep). Sex differences may also lead to differences in growth rates. We did not get enough sex and maturity data on our tagged fish to definitively assess these effects.

Recruitment

We expected brook trout recruitment to decrease as brown trout density increased across stream reaches. However, the effect of brown trout density on brook trout recruitment was difficult to assess because age-0 brook trout didn't fully recruit to electrofishing gear until fall. Therefore we cannot say what reach they originated from. Because we saw downstream movement of age-0 from fall thru spring, it is possible this migration was taking place during their first spring and summer, thereby lessening the numbers of age-0 present in the headwater reaches by the time we sampled them in the fall. However, Hudy et al. (2010) didn't observe much dispersal of age-0 brook trout during the first 4 months of life. Nor did we identify any direct competition during spawning (see Grant et al. 2002). Recruitment for both species was less in all reaches during 2007 and may have been due to the March flood. A similar result is reported in Waters (1999) where a March flood presumably reduced that year-class of brook trout. Given the large range in recruitment of brook trout across three years, it is likely that recruitment is set by environmental factors that can outweigh competition with brown trout. However, brown trout recruitment was much higher on a streamwide basis than it was for brook trout. So although brook trout recruitment varied presumably by environmental conditions, it still may have been dampened by presence of brown trout.

Movement

Reach was important for movement for all age classes of brook trout with age-0 moving downstream into lower reaches, but then emigrating out of these same reaches as adults. Age-0 brook trout move more extensively than adults and their dispersal rate increases with overall abundance (Hunt 1965). Brook trout in lower reaches were maintained in low numbers by immigration of age-0 from upper reaches. Movement of adult brook trout out of brown trout reaches could be an indication of forced emigration. Alternatively, upstream movement of adult trout could have been related to avoiding warmer water temperatures in the summer or to find spawning areas in the fall. However, this is unlikely given that there was not a seasonal component to movement, water temperatures did not get above optimal limits, and there was suitable spawning habitat in the lower reach. Emigration due to intraspecific competition has been demonstrated for salmonids, but there is less evidence of forced emigration caused by interspecific competition. This may be because in studies examining interspecific competition in the laboratory, subordinate species are not allowed to emigrate (closed systems). In field studies, emigration may not have been measured, but rather was incorporated into survival estimates. The fact that we did not see emigration of age-2+ brook trout in Hemmingway Creek is likely a function of study design. Movement was less for all age groups in Hemmingway Creek versus Coolridge Creek which is likely an artifact of not being able to sample the middle portion of Hemmingway Creek.

We did not observe consistent seasonal movements as seen in some studies with stream salmonids. Trout often move in fall to suitable spawning areas near headwaters of streams or to avoid warmer water temperatures in the summer. The fact that we did not observe seasonal movements, but rather consistent movements of adults upstream, suggests that movement was not driven by changing abiotic factors. Rather, we think this movement represented forced emigration of brook trout out of the brown trout dominated reaches.

Over half of the brook trout in our study showed site fidelity. Strange et al. (2000) found that most brook trout and brown trout moved less than 75m in a Tennessee stream. Limited movement may be caused by the presence of a competing species. Whitworth and Strange (1983) found very little movement of brook trout in sympatry with rainbow trout. Likewise, brown trout were responsible for limited movement of cutthroat trout (McHugh and Budy 2006). Movement rates of both brown trout and brook trout were low (5%) in sympatric population in Massachusetts (Carlson and Letcher 2003). Krueger and Menzel (1979) found genetic differences among brook trout populations in nearby streams suggesting only limited movement of brook trout among streams. Although a large portion of our trout did not move, those that did moved across study reaches and streams. This could be important in terms of recolinization and genetic diversity.

Survival

Surprisingly, survival of brook trout did not differ between reaches with high and low brown trout densities. Similarly, survival rates for cutthroat trout were similar in an experimental study with high versus low brown trout density (McHugh and Budy 2006); but the authors of that study attributed this finding to not effectively sampling small trout or due to limited length of study period. In a field study however, cutthroat trout survival was higher in areas without brown trout than in areas with brown trout (Budy et al. 2007). The discrepancies across studies points out the need for further research in this area. Interestingly, conventional methods for estimating survival likely would have shown lower survival in the brown trout reaches if we had not accounted for movement. While, predation on juvenile brook trout by large brown trout could be a mechanism where age-0 brook trout populations are reduced in sympatry with brown trout (Alexander 1977), survival estimates were similar in regards to brown trout presence for this age group in our study.

Survival of salmonids can often vary seasonally; however, there is little consensus as to what season is limiting, if any. For example, it has been suggested that winter can be a time of poor survival for salmonids (Brown et al. 2011). Whereas, Berger and Gresswell (2009) found that fall was the lowest period of survival for cutthroat trout. Similarly, survival varied by season for both brown trout and brook trout in a Massachusetts stream, with the lowest survival in fall and summer (Carlson and Letcher 2003). Summer can be a limiting time of survival when water temperatures are high (Xu et al. 2010a). Our study in combination with previous work, suggests that there might not be a critical time period for trout survival, but rather dependent on conditions during each season. Seasonal survival appeared to be driven by flood events which is consistent with previous findings in Minnesota and elsewhere (Waters 1999). High discharge can have negative effects on trout survival (see Budy et al 2008, pg 563 for review). Waters (1999) noticed a brook trout population to decline after severe flooding.

Environmental factors could have limited interspecific competition during this study. Hearn (1987) suggests that field studies of competition during periods of low trout density caused by environmental extremes (flooding in this case) may not provide an accurate assessment of interspecific competition. Competition among salmonids can often times be regulated by abiotic conditions (Taniguchi et al. 1998; McHugh and Budy 2005; Magoulick and Wilzbach 1998b). Conversely, when fish densities are high (increasing competition), biotic factors can outweigh abiotic factors in structuring trout populations (Quist and Hubert 2005). Given the myriad abiotic factors that can mediate competition among salmonids, it is important to gain a better understanding of these mechanisms when developing conservation plans.

Our high annual mortality rates may have been due to the large flooding events throughout our study. However, these results were similar to those found in Appalachian streams in terms of both annual mortality rates and life expectancy (Petty et al. 2005; Whitworth and Strange 1983). Likewise, few trout lived past three years given high mortality rates in Wisconsin (Brasch et al. 1973). However, in Colorado, where brook trout are considered an invasive species, they lived to as old as 14 years (Kennedy et al. 2003). Whether the mortality rates in our study are due solely to environmental conditions, or are being influenced by brown trout are not fully understood.

Longitudinal patterns

We saw similar patterns of fish distribution as reported for other systems, in that brook trout were primarily confined to headwater reaches and brown trout dominated the downstream reaches. Given the abundance of cover for adult trout and larger pool area found in the lower reaches, brook trout populations should not have been limited by habitat. Brown trout, however, had higher densities in lower reaches, as one would expect. Patterns were the same for bull trout (*Salvelinus confluentus*) and non-native brook trout in Idaho streams (Rieman et al. 2006). While temperature mediated competition has often been suggested as a mechanism (see Taniguchi and Nakano 2000), recent evidence does not support this idea (McHugh and Budy 2005). Because water temperatures were similar between upper Hemingway (brook trout dominated) and lower Coolridge (brown trout dominated), we would agree that temperature does not appear to be causing this distributional pattern. Although, laboratory studies show that brook trout are better competitors at lower water temperatures (Magoulick and Wilzbach 1998a). In a laboratory stream study, brook trout were located in upstream positions and chased brown trout downstream (Fausch 1981). It could be that brook trout are better suited for headwater reaches given their life history characteristics (Öhlund et al 2008). However, Magoulick and Wilzbach (1998b), found that brook trout were not better adapted to upstream reaches compared to middle and lower elevation reaches, but suggested that competition with rainbow trout in combination with habitat differences likely explained distributional patterns. Because brook trout are found in lower reaches to some extent, it is most likely that habitat is not limiting, but competition with brown trout is influencing brook trout abundance in Driftless area streams.

Conclusions

Competition can be age or size dependent; our results show evidence for adult interactions, but not age-0. Our results suggest that brown trout may be influencing adult brook trout distribution through forced emigration. Also, decreased growth rates of adult brook trout in the presence of brown trout warrant further research investigating possible mechanisms for this result. Although water temperatures were similar in two reaches, with and without abundant brown trout, we still cannot eliminate potential habitat differences across the reaches. There is still a question as to whether brook trout are being replaced by brown trout given habitat preferences in the lower reaches or displaced due to competition. Therefore, this study should be followed up by manipulative experiments to separate out habitat versus competition.

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Table 1. Fall population estimates, N/ha (SE) for brown trout and brook trout in four coldwater stream reaches in southeastern Minnesota. Streams reaches are upper (UH) and lower Hemmingway (LH), and upper (UC) and lower Coolridge (LC).

	Brook trout		Brown trout	
Stream reach	Adult	Age-0	Adult	Age-0
		2006		
UH	78.9 (5.3)	561.8 (13.8)	19.3 (na)	528.8 (18.5)
LH	99.2 (9.0)	378.0 (19.6)	1197.0 (42.6)	1122.8 (21.6)
UC	306.5 (24.0)	753.7 (37.0)	198.2 (8.7)	525.4 (15.2)
LC	89.9 (5.5)	192.3 (8.9)	727.4 (6.7)	2281.9 (56.5)
		2007		
UH	300.0 (73.6)	0 (0.0)	196.9 (37.9)	0 (0.0)
LH	209.1 (288.0)	9.5 (na)	1283.4 (184.7)	146.3 (49.3)
UC	521.3 (2.6)	141.8 (24.3)	382.7 (12.7)	90.4 (11.1)
LC	178.6 (3.8)	32.4 (1.4)	717.3 (24.5)	657.2 (33.3)
		2008		
UH	171.8 (na)	73.6 (na)	98.2 (na)	0 (na)
LH	134.2 (na)	109.8 (163.7)	1452.9 (36.6)	1321.1 (191.2)
UC	272.6 (22.6)	65.4 (12.2)	110.4 (26.0)	264.9 (13.5)
LC	88.0 (6.7)	114.9 (13.5)	633.3 (26.9)	2129.6 (53.9)

Table 2. Capture-recapture matrix combined for all stream reaches and age groups used to estimate survival and movement of brook trout. Numbers of fish are after accounting for tag loss.

						Recaptures					
Release occasion	Time period	Released (N)	2 (Nov 2006)	3 (Mar 2007)	4 (May 2007)	5 (Sep 2007)	6 (Nov 2007)	7 (Mar 2008)	8 (May 2008)	9 (Aug 2008)	10 (Oct 2008)
1	Sep. 2006	226	90	55	46	25	12	10	10	10	8
2	Nov. 2006	1		0	0	0	0	0	0	0	0
3	Mar. 2007	130		0	52	20	12	8	7	7	12
4	May. 2007	0			0	0	0	0	0	0	0
5	Sep. 2007	168				0	59	63	44	35	34
	Total	525	90	55	98	45	83	81	61	52	54

Table 3. Ranking of multistrata Cormack-Jolly-Seber models estimating survival (S, where t denotes time, treat denotes treatment as BNT density), capture probability (p, where r denotes reach, t denotes season), and movement (Ψ, where subscripts are the same as for S and p) for three age groups of brook trout. 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 (Δ_i < 2) are highlighted in bold.

Model	AIC_c	ΔAIC_c	w_i	*K*	Deviance
		Age -0			
S(.)p(r)Ψ(r)	**803.23**	**0.00**	**0.62**	**17**	**129.77**
S(treat)p(r)Ψ(r)	**804.85**	**1.62**	**0.28**	**18**	**129.17**
S(r)p(r)Ψ(r)	807.87	4.64	0.06	20	127.72
S(t)p(r)Ψ(r)	808.84	5.61	0.04	20	128.69
S(treat*t)p(r)Ψ(r)	812.42	9.19	0.01	24	123.16
S(r*t)p(r)Ψ(r)	819.72	16.49	0.00	32	111.55
S(r*t)p(r*t)Ψ(r*t)	916.52	113.29	0.00	77	81.96
		Age-1			
S(t)p(t)Ψ(r)	**1314.52**	**0.00**	**1.00**	**25**	**270.28**
S(treat*t)p(t)Ψ(r)	1328.89	14.38	0.00	32	269.11
S(.)p(t)Ψ(r)	1331.64	17.12	0.00	20	298.26
S(treat)p(t)Ψ(r)	1333.00	18.49	0.00	21	297.47
S(r)p(t)Ψ(r)	1336.67	22.15	0.00	23	296.80
S(r*t)p(t)Ψ(r)	1350.59	36.08	0.00	46	258.47
S(r*t)p(r*t)Ψ(r*t)	1545.15	230.64	0.00	133	205.37
		Age-2+			
S(t)p(.)Ψ(r)	**862.46**	**0.00**	**0.98**	**22**	**321.65**
S(treat*t)p(.)Ψ(r)	870.46	8.01	0.02	31	308.52
S(r)p(.)Ψ(r)	878.96	16.50	0.00	17	349.40
S(.)p(.)Ψ(r)	881.60	19.14	0.00	14	358.63
S(treat)p(.)Ψ(r)	883.36	20.90	0.00	15	358.20
S(r*t)p(.)Ψ(r)	886.57	24.11	0.00	49	278.57
S(r*t)p(r*t)Ψ(r*t)	1333.39	470.93	0.00	164	220.70

Table 4. Parameter estimates and unconditional standard errors based on the most supported multi-strata Cormack-Jolly-Seber models for apparent survival (S), capture probabilities (p), and movement (Ψ) for three age classes of brook trout in four coldwater stream reaches in southeast Minnesota. Age-0 parameter estimates are model averaged over the top two competing models. Movement estimates only shown if greater than 1%.

Parameter	Estimate	± SE
Age-0 estimates from S(treat)p(r)Ψ(r) and S(.)p(r)Ψ(r)		
S – High BNT density	0.69	0.05
S – Low BNT density	0.71	0.04
p – LC	0.64	0.15
p – UC	0.46	0.13
p – LH	0.35	0.05
p – UH	0.55	0.06
Ψ – LC to UC	0.06	0.07
Ψ – LC to LH	0.08	0.08
Ψ – UC to LC	0.12	0.07
Ψ – LH to UH	0.01	0.01
Ψ – UH to LH	0.04	0.02
Age-1 parameter estimates from S(t)p(t)Ψ(r)		
S – Fall 06	1.00	0.00
S – Winter 06-07	0.53	0.07
S – Spring 07	0.70	0.12
S – Summer 07	0.41	0.08
S – Fall 07	0.57	0.05
S – Winter 07-08	0.84	0.05
p – Fall 06	0.38	0.06
p – Winter 06-07	0.78	0.11
p – Spring 07	0.59	0.09
p – Summer 07	0.61	0.10
p – Fall 07	0.55	0.06
p – Winter 07-08	0.72	0.06
Ψ – LC to UC	0.10	0.03
Ψ – LC to LH	0.01	0.01
Ψ – UC to LC	0.04	0.02
Ψ – LH to UH	0.04	0.02
Ψ – UH to LH	0.02	0.01
Age-2+ parameter estimates from S(t)p(.)Ψ(r)		
S – Fall 06	0.94	0.25
S – Winter 06-07	0.45	0.13
S – Spring 07	0.88	0.13

Table 4 continued…

S – Summer 07	0.51	0.09
S – Fall 07	0.63	0.08
S – Winter 07-08	1.00	0.00
S – Spring 08	0.88	0.06
S – Summer 08	0.89	0.06
p	0.60	0.03
Ψ – LC to UC	0.12	0.04
Ψ – UC to LC	0.07	0.03

Table 5. Habitat measurements for upper and lower reaches of Coolridge and Hemmingway Creeks. Mean (±SE) wetted width, depth, and discharge taken during baseflow conditions. Fines is the percent of stream bottom substrate composed of fine sediment. Trout cover is the percent pool area with in-stream rock, instream vegetation, overhead bank, wood, and water depths greater than 1m. July water temperatures are monthly means (±SE).

									July (°C)	
Stream	Reach	Length (m)	Wetted Width (m)	Depth(cm)	Discharge (m^3/s)	Fines (%)	Slope (%)	Trout cover (%)	2008	2009
Coolridge	Upper	515	2.72 (0.27)	12.5 (0.91)	0.03 (0.00)	17.3	2.60	5.80	11.43 (0.07)	10.59 (0.04)
	Lower	1085	3.52 (0.16)	16.46 (0.91)	0.06 (0.01)	25.5	1.50	4.60		11.67 (0.07)
Hemmingway	Upper	730	3.44 (0.16)	21.34 (3.05)	0.06 (0.02)	18.3	1.07	11.60	11.45 (0.06)	
	Lower	935	4.17 (0.18)	37.2 (3.05)	0.11 (0.01)	41.0	0.75	18.37	13.85 (0.09)	13.24 (0.11)

Figure 1. Map of study area showing five stream reaches. Upper Hemmingway (UH) and Upper Coolridge (UC) are brook trout dominated with low brown trout density, whereas lower Hemmingway (LH), lower Coolridge (LC), and Pine (P) are brown trout dominated.

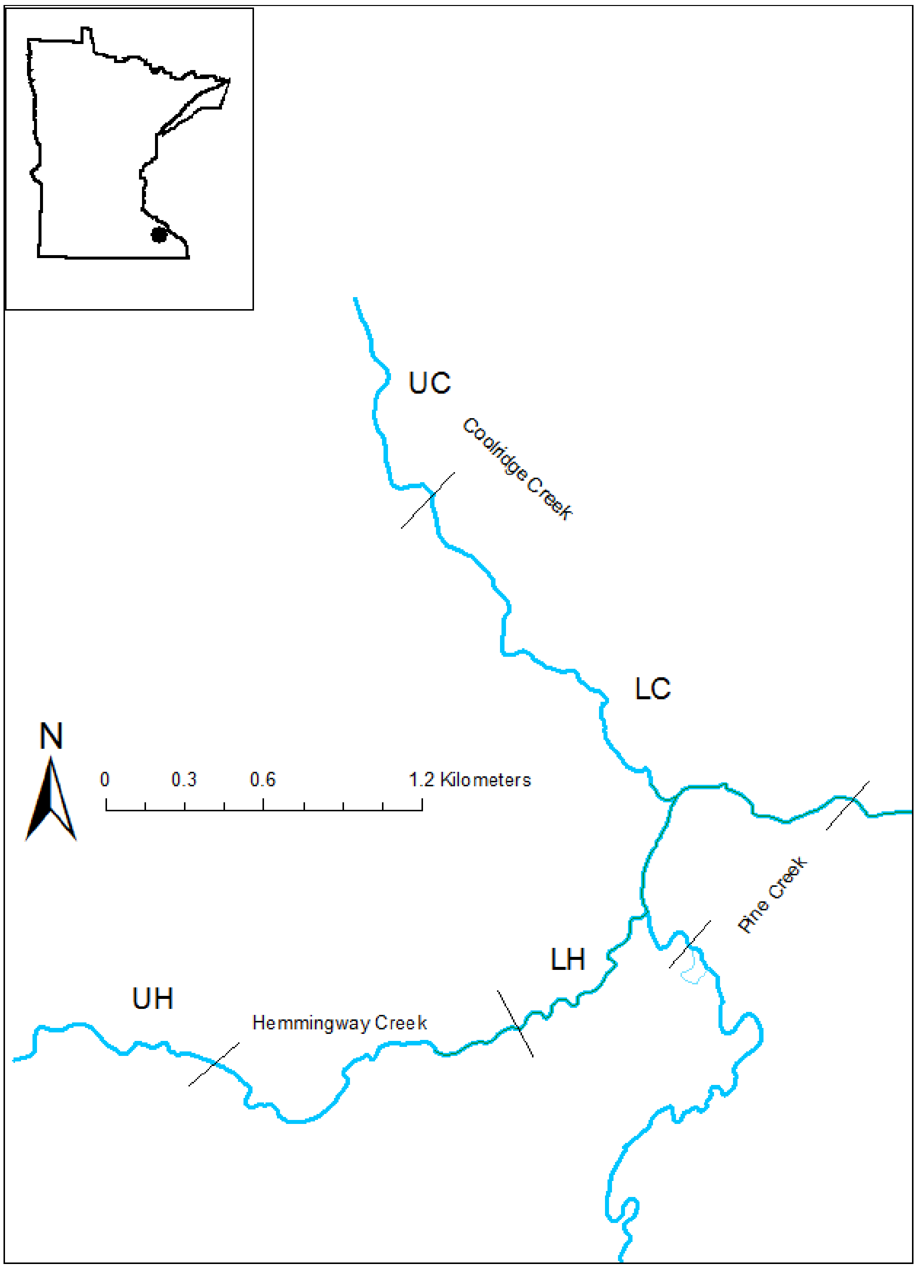


Figure 2. Length frequency histograms of sampled brook trout used to assign age groups for three marking occasions for Coolridge Creek.

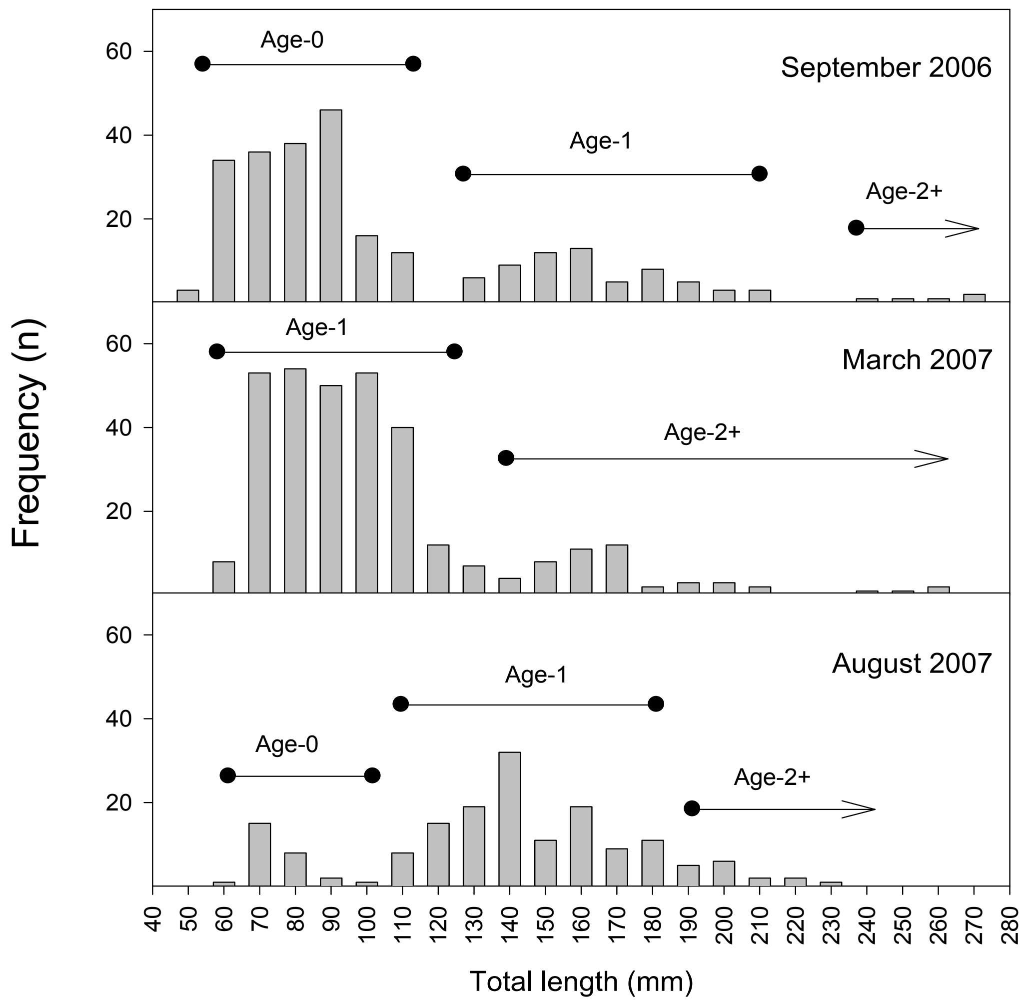


Figure 3. Length frequency histograms of sampled brook trout used to assign age groups for three marking occasions for Hemmingway Creek.

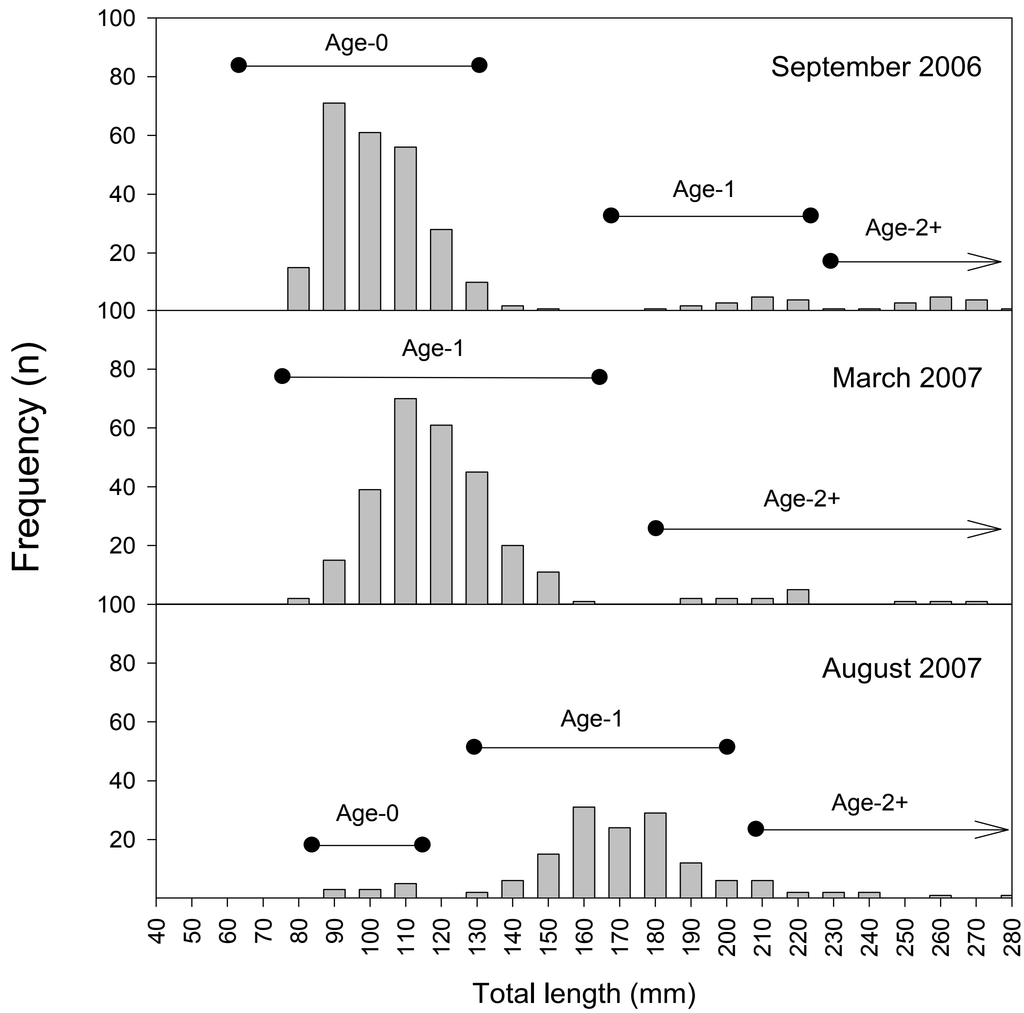
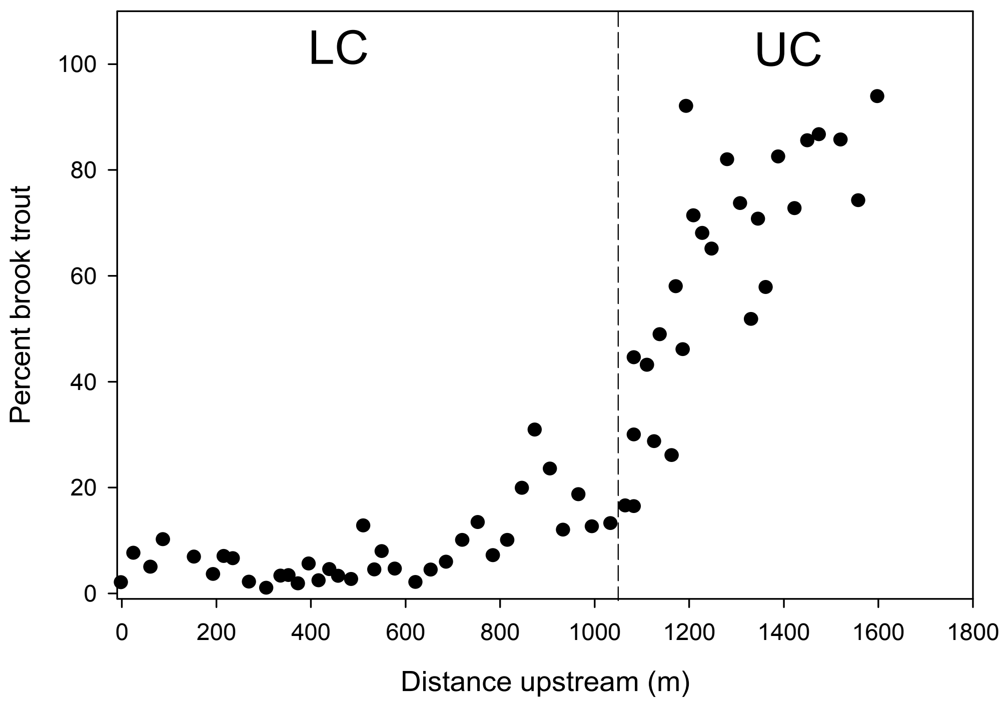


Figure 4. Percent of trout population comprised of brook trout in relation to distance upstream. Each data point represents an individual pool.



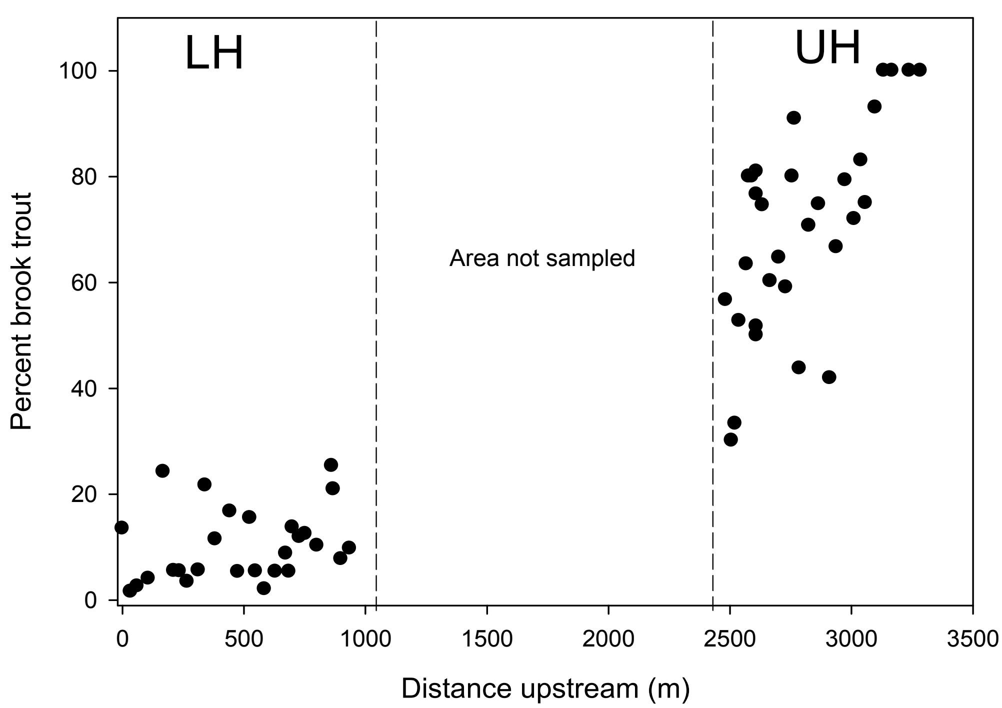


Figure 5. Seasonal growth of three size classes of brook trout in Coolridge and Hemmingway creeks.

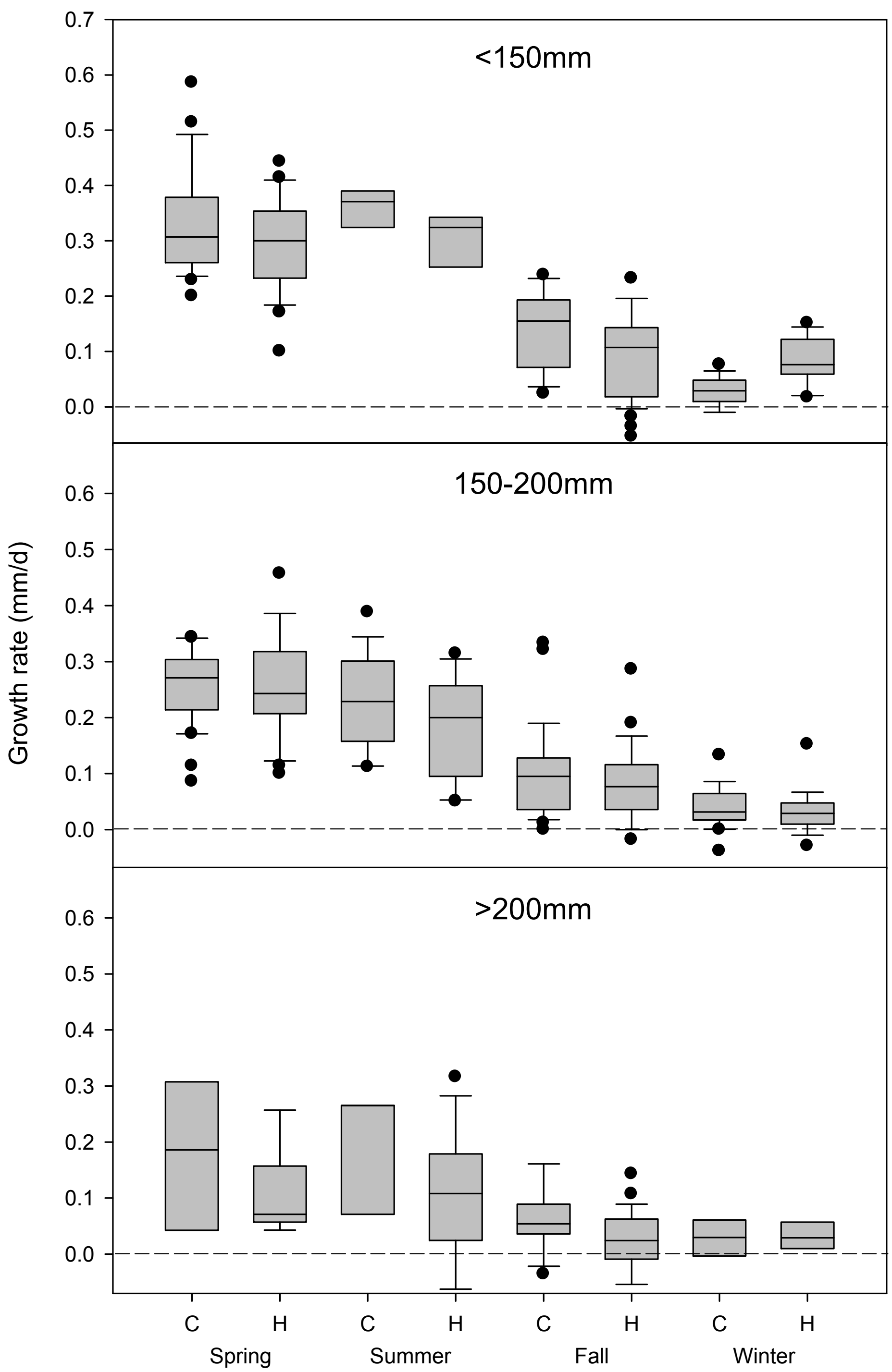


Figure 6. Growth rates (spring and summer combined) of three size classes of brook trout collected in stream reaches with high (LH, LC) or low (UH, UC) brown trout densities.

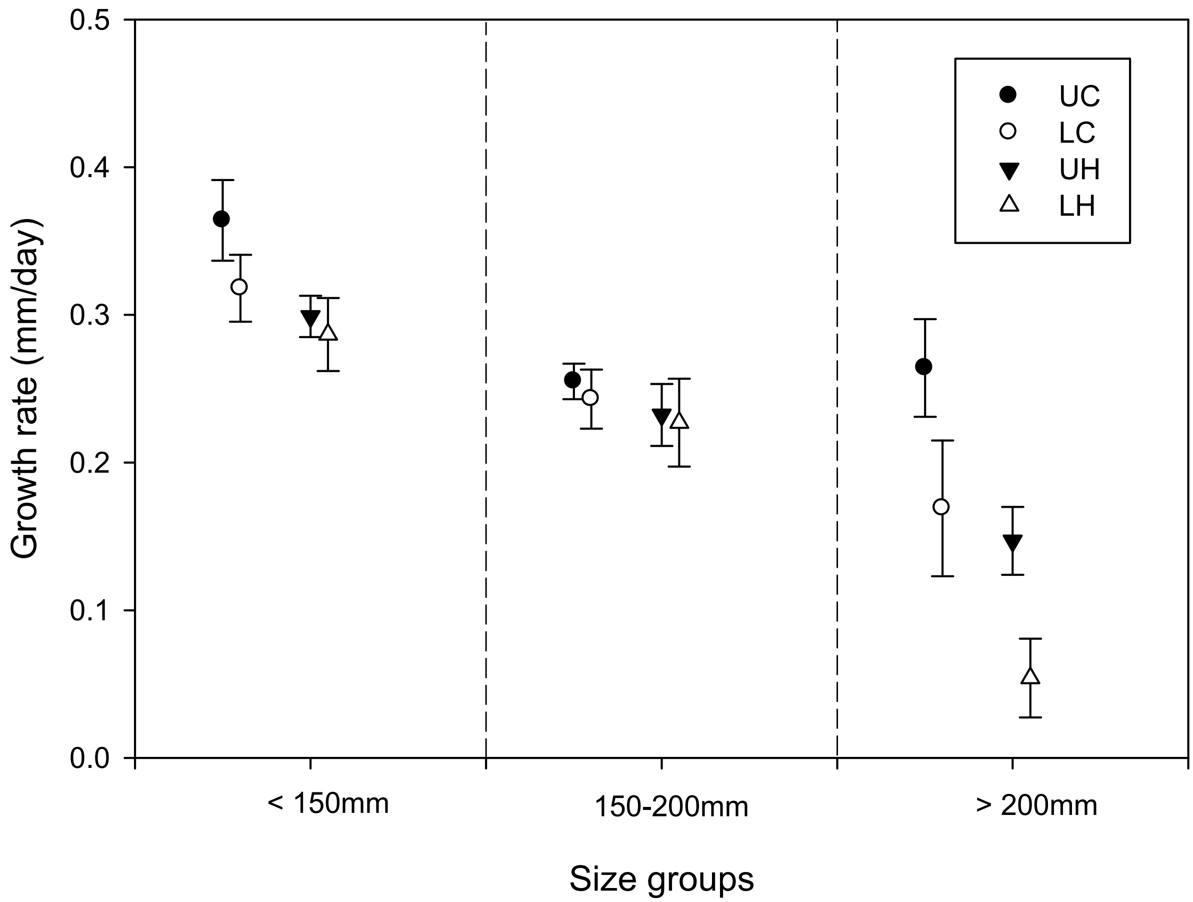


Figure 7. Observed growth of 2006 year-class of brook trout in Coolridge and Hemmingway creeks.

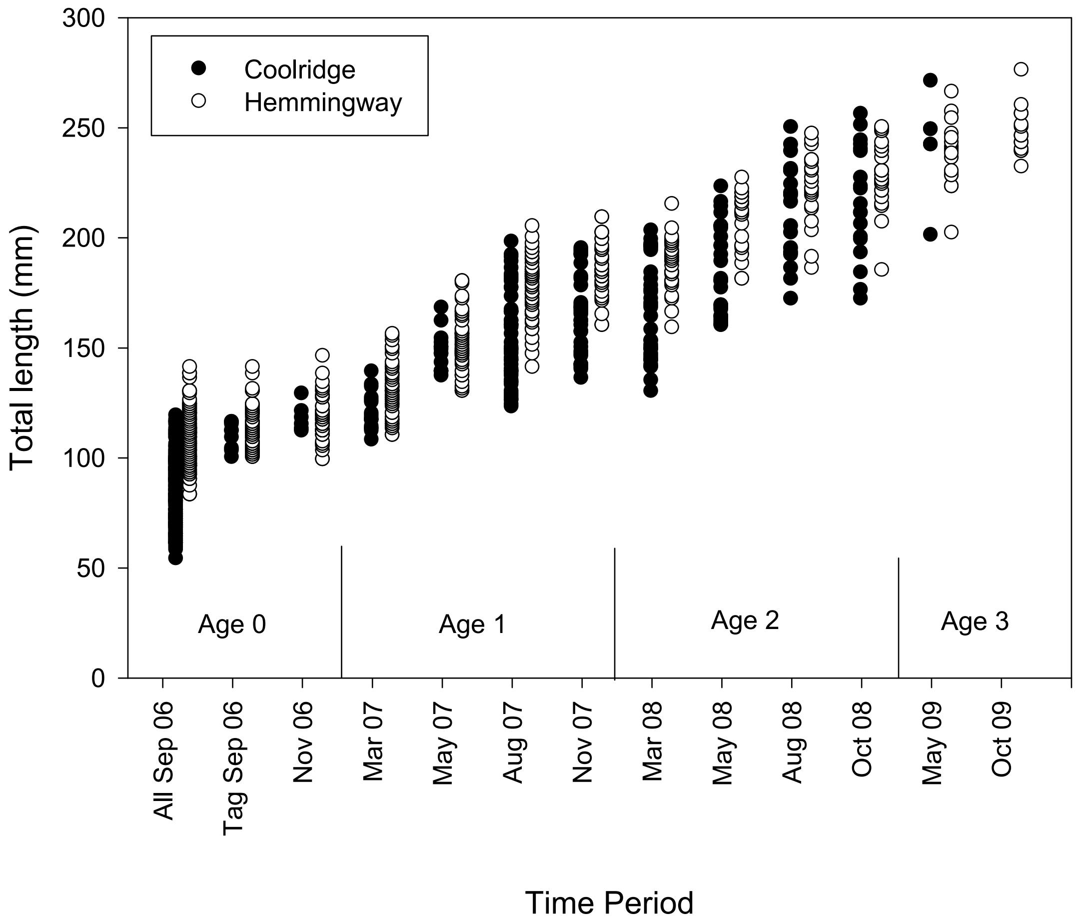


Figure 8. Seasonal movement rates of three age classes of brook trout between reaches with high (LH, LC) or low (UH, UC) brown trout densities. Only movement rates greater than 0.5% are shown (thick arrows represent rates over or equal to 10%).

Figure 9. Survival estimates and standard error bars generated from Program MARK for three age classes of brook trout across all reaches.

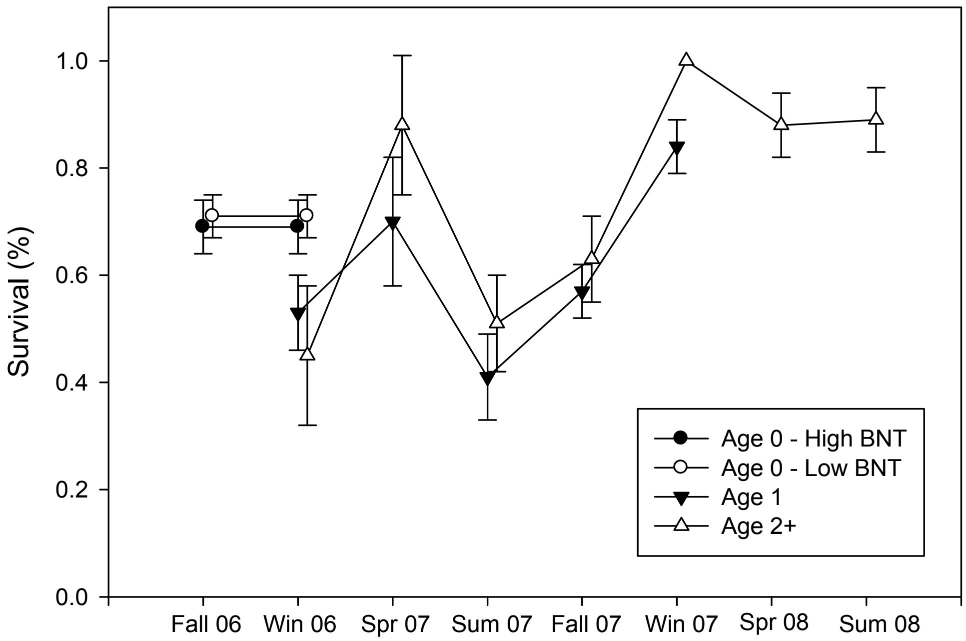


Figure 10. Regional discharge data (m^3/s) gathered from the closest monitoring gage in the watershed, located 34km downstream in the Root River, a 6th order stream.

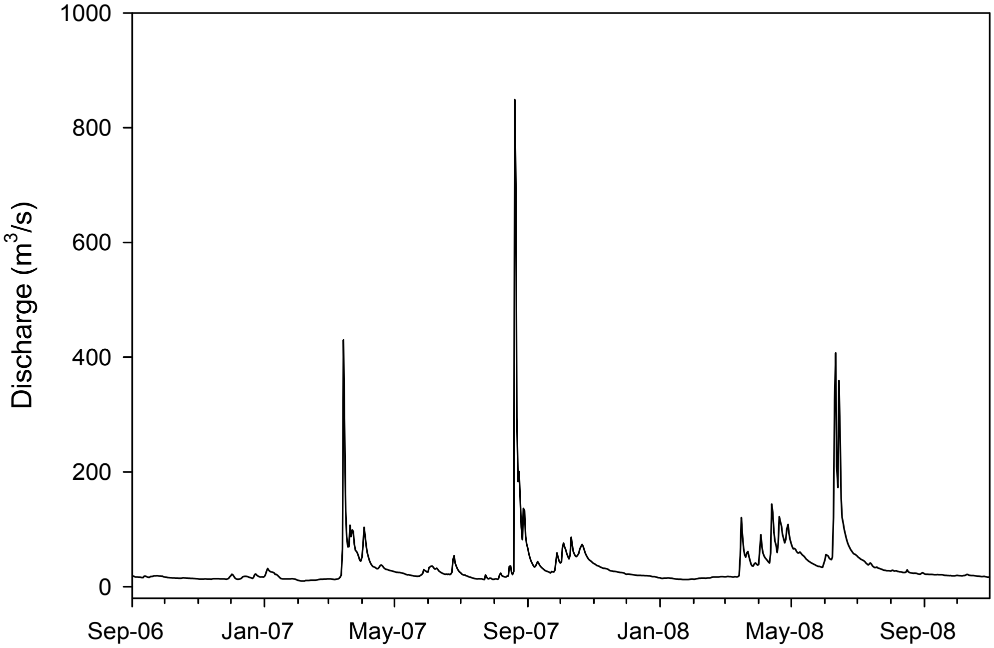
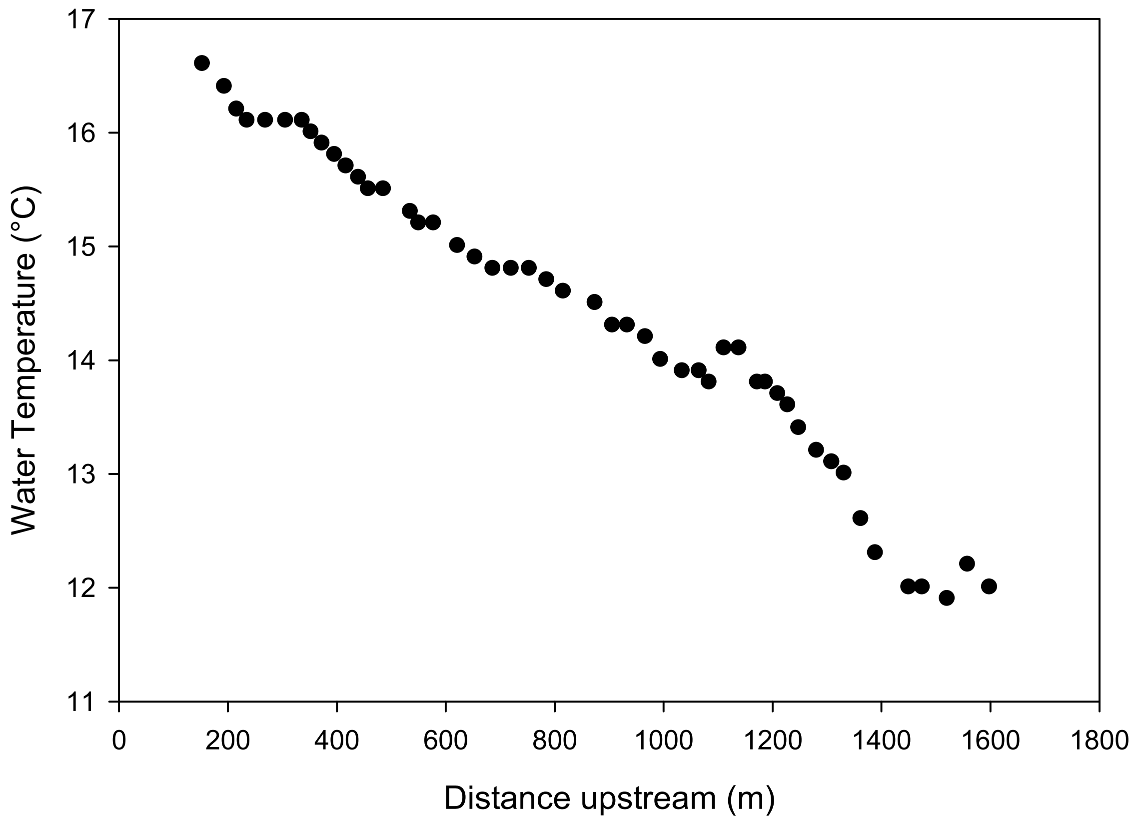


Figure 11. Longitudinal water temperature (°C) profile taken in Coolridge Creek on 8/14/2009 showing temperature changes from the source to the mouth.



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