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Brown trout *Salmo trutta* growth and condition along a winter thermal gradient in temperate streams

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Abstract

Winter harshness and the degree to which it can impact stream dwelling salmonid populations has received considerable attention from fisheries biologists, although some debate exists regarding the importance of winter severity for local populations. Groundwater input may buffer stream water temperature and benefit fish in buffered vs. unbuffered streams. Overwinter growth and condition of individual brown trout were measured in 24 groundwater-dominated streams, and the relations between winter growth and condition to stream thermal regime (quantified by regressions of air and water temperature) and diet quality (amount and caloric density of prey) were examined in a subset of 16 streams. Brown trout growth rate ($\text{mg} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) was positive overwinter in 18 of 24 streams, and there was no significant change in condition between early and late winter. Juvenile fish grew faster than adults, but there was no significant difference in condition between adults and juveniles. Thermal regime positively influenced winter growth for both adults and juveniles, likely mediated through moderation of water temperature by groundwater, whereas diet had no significant effect on growth.

Keywords: groundwater, thermal buffering, winter growth

Introduction

Considerable debate exists about the influence of winter conditions on salmonid populations, especially stream-resident brown trout *Salmo trutta* (Huusko et al. 2007; Carlson et al. 2008). Some have argued that winter can be a stressful time period due to loss of important habitat features, low water temperatures and decreased availability of drifting and terrestrial invertebrate prey (Brown et al. 2011; Weber et al. 2013). Substantial ice formation, especially of anchor ice, can reduce availability of important winter habitat features such as deep pools and interstitial spaces in cobble and rubble substrates (Huusko et al. 2007; Jonsson and Jonsson 2011; Brown et al. 2011). Declining water temperatures may decrease the burst swimming speed of salmonids hindering their ability to avoid endothermic predators or to capture prey (Brown et al. 2011; Jonsson and Jonsson 2011). Low winter water temperatures coupled with declining prey abundance can lead to depletion of lipid energy reserves and in turn result in fish with lower condition and decreased body mass or growth. Such patterns have been noted in rainbow trout *Oncorhynchus mykiss* (Biro et al. 2004), brook trout *Salvelinus fontinalis* (Xu et al. 2010) and brown trout (e.g., Kelly-Quinn and Bracken 1990; Berg and Bremset 1998; Koljonen et al. 2012). Should these stressful winter conditions persist, salmonid mortality could be high during this season (Lund et al. 2003; Huusko et al. 2007; Linnansaari and Cunjak 2010).

Conversely, empirical evidence from several studies indicate that overwinter mortality of salmonids may not be the critical seasonal bottleneck it was once believed to be (Huusko et al. 2007; Carlson et al. 2008; Dieterman and Hoxmeier 2011; Lobón-Cerviá et al. 2012). Huusko et al. (2007) noted that published estimates of winter survival were substantially variable

among lotic populations and likely related to differences in winter conditions among rivers. Populations that exhibit higher winter survival might also be expected to have individuals with higher lipid content, good growth and in better condition than populations with lower survival. For example, brown trout in three streams in southeastern Minnesota, USA had highest seasonal survival during winter and exhibited positive growth in length during this season (Dieterman and Hoxmeier 2011; Dieterman et al. 2012). Other studies have reported no or negligible winter growth (e.g., Nicola and Almodóvar 2004) or even structural growth reductions that led to decreased winter survival (e.g., Johnsson and Bohlin 2006; Huusko et al. 2011). Few studies have empirically examined the winter conditions that might be associated with spatial differences in winter survival, growth or condition among populations, although many researchers have logically suggested that water temperature and diet are likely important (Carlson et al. 2008; Jonsson and Jonsson 2011).

Water temperature is one of the primary modifiers of brown trout energetics, growth, condition, and survival, especially during summer months (e.g., Elliott 1994; 2009; Jensen et al. 2000; Jonsson and Jonsson 2011). Air temperature is a primary modifier of water temperature, particularly in temperate lotic systems (e.g., Erickson and Stefan 2000; Morrill et al. 2005). However, streams with hydrologic regimes dominated by groundwater input may experience substantially different thermal regimes than surface water-dominated streams, significantly impacting trout populations (Nicola and Almodóvar 2004; O'Driscoll and DeWalle 2006). For example, Nicola and Almodóvar (2004) found faster brown trout growth in groundwater-dominated streams than in surface-water dominated streams in central Spain.

Thermal regime differences between groundwater-fed and surface-water-fed streams may be even more pronounced in winter (Krider et al. 2013). Groundwater inputs commonly result in more stable thermal regimes across all seasons than surface-water fed streams (e.g., Nicola and Almodóvar 2004). Consequently, groundwater inputs can provide thermal refugia for stream trout during winter, much as they provide cool water refuges during summer. The winter-warm conditions of groundwater input have been associated with increased winter survival of brook trout in Wisconsin, USA (Hunt 1969) and rainbow trout in Idaho, USA (Smith and Griffith 1994), although differing preference by species for proximity to groundwater discharge points was reported by Cunjak (1996). Groundwater input buffers water temperature, reduces or prevents ice formation, and can maintain higher base flows in winter. However not all groundwater-fed streams receive the same amount of groundwater input. Therefore, winter severity among streams within a region may vary depending on the amount of groundwater input received, resulting in spatial differences in salmonid growth, condition or survival.

Winter diet of brown trout may be important modifiers of condition, growth and survival because trout are known to continue feeding during winter months in many streams (e.g., Heggenes et al. 1993; Jonsson and Jonsson 2011; French et al. 2014; Anderson et al. 2016). For example, age-1 brown trout in the Vosso River, Norway fed on Plecoptera, Trichoptera and Diptera larvae and pupae in December (Jonsson and Jonsson 2011). French et al. (2014) found Amphipoda, Diptera and Trichoptera to be common prey in winter-feeding brown trout in one Minnesota stream. The energy density of the different prey taxa may be as important as the overall abundance of prey ingested because reduced gastric evacuation rates

at lower water temperatures can reduce trout consumption rates and result in a net loss of energetic intake (Elliott 1972; Cunjak and Power 1987; Cunjak et al. 1987). Anderson (2012) found that the winter availability of different invertebrate taxa and their abundances were extremely variable among 18 groundwater-fed streams in southeast Minnesota. Thus, the abundance of invertebrate prey consumed or the energy density of different taxa consumed could differ among streams as well and in turn, explain spatial differences in salmonid condition, growth or survival among streams during winter.

Associations between salmonid growth, condition, thermal stability, and trout diets across a winter gradient of groundwater input have rarely been examined and usually limited to a small number of streams. The Driftless Area of southeastern Minnesota, USA, so named because the most recent glaciation missed all or most of the region and did not deposit drift, i.e., fine material deposited on adjacent land areas that were glaciated (Hobbs 1999); contains numerous groundwater-fed trout streams (Thorn et al. 1997; Hoxmeier et al. 2015). These streams have varying thermal stability indicative of differing groundwater inputs (Kridler et al. 2013).

In this study, growth rate and condition of brown trout were examined in 24 of these groundwater-dominated streams in winter; significantly broader in scope than most previous studies. We sought to determine whether (1) brown trout maintained positive growth and good body condition over winter in these groundwater-fed streams and (2) were spatial differences in winter growth or condition associated with either thermal stability, abundance of invertebrates in the diet or energetic diet differences.

128 **Methods**

129 *Study area*

130 The Driftless Area region is characterized by karstic geology, with a large number of
131 groundwater-dominated streams that support cold-water fishes and invertebrates (Figure 1).
132 These streams support an important recreational fishery, primarily for brown trout, although
133 rainbow trout and native brook trout are also present in some streams (Thorn et al. 1997;
134 Gartner et al. 2002; Snook and Dieterman 2014; Hoxmeier et al. 2015).

135 The 24 streams selected for this study supported naturalized populations of brown trout
136 and no supplemental stocking of brown trout occurred. Rainbow and brook trout were absent
137 or present in low numbers (5 or fewer captured per stream) in all streams except Trout Valley
138 Creek where brook trout made up the majority of fishes sampled. Winter angling between
139 January 1 and March 31 was available on 11 of the 24 streams but no harvest of trout was
140 allowed. Sampling sites consisted of a 150m reach of stream containing multiple pools, riffles,
141 and runs. Sites were selected to be wadeable, effectively sampled by a backpack electrofisher,
142 and maximum stream wetted width was between 2m and 15m (Table1). Groundwater input
143 from springs maintained stream water temperatures above freezing and prevented ice
144 formation at most sampling sites during this study.

145 *Fish, growth, and condition*

146 To quantify winter growth and condition we collected brown trout from selected
147 streams during the winters of 2010-13 using backpack electrofishing gear (Smith Root;
148 Washington, USA; LR 20B) (Table 1). Fish were typically collected during a single electrofishing

pass without blocking nets, although additional passes were made if sample sizes were low. Each stream was sampled during early (November-December) and late (February-March) winter for a total of two sampling events per stream. After collection fish were placed in holding pens, anesthetized with an immobilizing dose of tricaine methanesulfonate (MS 222), weighed $\pm 1\text{g}$ and measured $\pm 1\text{mm}$. Between 22 and 151 randomly selected trout per stream collected during early winter were tagged in the anterior portion of the body cavity with 9mm passive integrated transponder (PIT) tags (Biomark Inc.; Idaho, USA). Growth rate was measured from recaptured individuals as the change in body weight as a function of initial body weight and the number of days elapsed between early and late sampling events (i.e., $\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$). Fish condition (a measure of fish health or “plumpness”) was measured with the relative weight index (Wr). Relative weight compares the weight-at-length of a sampled fish to a regionalized standard weight for that species and values between 80 and 100 are generally considered acceptable for healthy populations (Anderson & Neumann 1996). Relative weight is a popular condition metric for North American fisheries managers, and allows comparisons of fish condition across populations and size classes (Blackwell et al. 2000). Standard weight equations developed by Milewski & Brown (1994) from 51 North American lotic brown trout populations were used to calculate Wr for fish in this study. Condition was only analyzed for brown trout $\geq 140\text{mm}$ total length; because the standard weight equation was not developed for smaller brown trout.

Thermal stability/groundwater input

To quantify thermal stability as a proxy measure of groundwater input we used a-priori data collected by Krider et al. (2013). Krider et al. (2013) constructed linear regression models of the air-water temperature relationship for 40 streams in southeastern Minnesota from weekly mean air and water temperatures over a minimum of 15 weeks. The parameters from these regressions were used by Krider et al. (2013) to classify stream temperature regime along a gradient as primarily influenced by groundwater or meteorological controls. We used slopes from the air-water temperature regression equations developed by Krider et al. (2013) for 16 of the 24 study streams as an estimate of groundwater input in this study. Slopes closer to one indicate a greater influence of air temperature on water temperature and less groundwater input, whereas slopes closer to 0 indicate a reduced influence of air temperature on water temperature, and more groundwater input. Streams with no existing air-water temperature regression (8 of 24) were excluded from analyses that included temperature. Regression slopes for our streams ranged from 0.178 in Big Springs Creek to 0.611 in Pickwick Creek. We selected streams to represent a range of groundwater input based in part on a-priori knowledge of air-water temperature relationships indicative of groundwater input for this study. The goal was to cover a range of stream thermal regimes typical of southeastern Minnesota trout streams. For example, predicted water temperature at a mean weekly air temperature of -10°C (a common mid-winter occurrence in southeastern Minnesota) via the Krider et al. (2013) equations ranged from 5.8°C for Big Springs Creek to 0.3°C for Pickwick Creek.

Abundance and energy content of invertebrate prey in brown trout diets

To estimate abundance and energy content of invertebrate prey in brown trout diets we used stomach contents collected from up to 30 individual trout per stream during the early and late winter sampling events in the 24 study streams (French 2014). Invertebrate taxa were identified and counted, and dry weight estimates were derived using equations published by Benke et al. (1999) and Méthot et al. (2012). Diet composition was incorporated into linear mixed-effects models to examine the effect of prey quantity and quality on winter growth. The most abundant prey taxa by dry weight in brown trout stomach contents were assigned to either high energy (>4000 J/g; *Gammarus*, Ephemeroptera, Plecoptera, *Physella*) or low energy (<3000 J/g; Diptera, Trichoptera) categories based on energy densities reported by Cummins and Wuycheck (1971). These values accommodated the six most abundant prey taxa while establishing a substantial difference in energy density (1000 J/g) between categories. These six prey taxa were also abundant in the diet of southeastern Minnesota brown trout as reported by French et al. (2014) and Anderson et al. (2016).

Analyses

Juvenile and adult growth rates were modeled separately to reduce bias from gamete production and spawning of adults in late autumn preceding the early winter sampling. Brown trout in the region typically reach maturity by 240 mm TL (Dieterman et al. In Press). Therefore, growth and condition were compared for two size categories: juvenile (<240 mm TL) and adult (> 240 mm TL) fish. Mean early winter and late winter W_r of recaptured juvenile and adult brown trout pooled across streams were compared with a 2-way ANOVA and pairwise t-test. The change in W_r for recaptured juvenile and adult brown trout pooled across streams was

compared with an unpaired t-test. Also, relationships between brown trout W_r and thermal stability were examined using linear regression.

Linear mixed-effects models fit by maximum likelihood were used to examine relationships between groundwater input, consumption, and diet quality on mean brown trout growth in 16 of the 24 streams. These models allowed a robust analysis of the data and accounted for random variation between sampling years, thus reducing potential bias. Mean brown trout growth was calculated by stream, and each stream was treated as a replicate. Fixed effects included: groundwater input, prey mass consumed and diet quality (prey energy density, Table 2). Year was modeled as a random effect. AICc was used to compare models to reduce the chance of over fitting due to small sample size and relatively few parameters (Burnham and Anderson 2002). All $\Delta AICc$ values were computed as the difference between the AICc of the model with the lowest AICc value and that of other models. Models with $\Delta AICc$ values >2.0 were considered significantly different from one another, and the model with the smaller AICc value is preferable (Burnham and Anderson 2002). AIC weights measure the amount of support (0-1) a particular model has from the data. Mixed-effects modeling was conducted using the lme function in the lme4 package in Program R (version 3.0.2)

Results

Growth and condition

We identified spatial gradients in both winter growth rate and condition of brown trout across the 24 streams. Juvenile fish were recaptured in all 24 streams, whereas adult fish were recaptured in 20 of 24 streams. Juvenile mean winter growth rate was positive in 18 of the 24

streams and ranged from $3.83 \text{ mg} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ in Cold Spring Brook, to $-1.66 \text{ mg} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ in Hay Creek (Figure 2). Adult mean winter growth rate was positive in 14 of 20 streams and ranged from $3.64 \text{ mg} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ in Hay Creek to $-1.64 \text{ mg} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ in Pickwick Creek. There was a large amount of variation in individual growth rate within a stream; for example, several fish in Pickwick Creek had positive winter growth rate, although mean growth rate was negative for Pickwick Creek fish. Juvenile fish typically grew faster than adults from the same stream. Recapture rates of tagged fish ranged from 5% in Beaver Creek to 45% in Spring Creek, and mean stream recapture rate was 22%.

Mean condition of brown trout was similar for adult and juvenile fish during early and late winter, and there was no significant change in condition between early and late winter for adult or juvenile brown trout (Figure 3). Relative weight calculations indicated fish were in generally good condition during winter, with mean W_r of 88.9 for all fish in early winter and 87.9 in late winter. Mean W_r values ranged from a high of 104.1 in early winter for Cold Spring Brook to 72.1 in late winter from Pickwick Creek. As no significant differences in W_r were found between juveniles and adults, values were pooled to examine the relationship between thermal regime and winter W_r .

There was a significant negative relationship between the slope of the air-water regressions and late winter mean brown trout condition (Figure 4). Trout in streams with smaller slopes, indicative of increased groundwater input, generally had greater W_r values than fish from streams with larger slopes. There was also a significant negative relationship between slope and overwinter change in W_r .

252 *Mixed effects modeling*

253 Thermal stability (estimate of groundwater input) was a coefficient in the top three
254 models of growth for juvenile and adult trout (Table 3). Sampling year, modeled as a random
255 effect, was not significant in any model. There was about 67% support for a singular effect of
256 thermal stability on juvenile growth and about 82% support for such an effect on adult growth.
257 Growth rate was inversely related with slope, suggesting that greater thermal stability in winter
258 had a positive effect on trout growth. Brown trout in streams with smaller slopes for air-water
259 regressions, indicative of increased groundwater input, had increased growth compared to fish
260 from streams more responsive to air temperature fluctuations. Addition of prey quality and
261 quantity variables did not improve model performance for juvenile ($\Delta AICc = 2.38$, $AICc$
262 weight=0.2), or adult growth ($\Delta AICc = 4.47$, $AICc$ weight = 0.09).

263 **Discussion**

264 Brown trout grew and maintained good condition over winter in most streams and
265 these biotic processes were associated more with increased thermal stability (as a proxy of
266 groundwater input) than invertebrate prey availability or energetic quality. Such information
267 accentuates the need to identify groundwater management zones and should influence the
268 prioritization of streams for management under a warming climate. Our study represents a
269 comprehensive assessment of the influence of thermal stability on brown trout growth and
270 condition during the winter in temperate North American streams.

271 Brown trout grew significantly during winter in the majority of streams (17 of 24)
272 sampled during this study. Similarly, Lobón-Cerviá and Rincón (1998), Nicola and Almodóvar

(2004), Dieterman et al. (2012), and French et al. (2014) observed growth of brown trout during winter. Watz et al. (2016) reported significant growth of brown trout while examining the effects of ice cover on growth in a stream in central Sweden, however the majority of this growth likely occurred during April and May as mean stream water temperatures ranged from 0.3-0.4 °C from December through March. Other studies have documented minimal or no growth of brown trout during winter in several systems including the Credit River, a Canadian tributary to Lake Ontario (Cunjak and Power 1987), the River Dodder, Ireland (Kelly-Quinn and Bracken 1990), West Brook Massachusetts, USA (Carlson et al. 2007), and in artificial stream experiments (Koljonen et al. 2012). Dissimilar stream temperature regimes likely contribute to the differences in growth observed across these studies (Table 4).

The relationship between air-water temperature regressions and brown trout growth suggests that water temperature buffered by groundwater input is an important factor governing growth. Winter water temperatures where brown trout grew during winter were either significantly buffered by groundwater input (Nicola and Almodóvar 2004; Dieterman et al. 2012; French et al. 2014), or mild local climate (Lobón-Cerviá and Rincón (1998). By contrast, studies where trout experienced no or minimal winter growth were conducted in streams with minimal groundwater buffering of water temperatures. For example, water temperatures were often just above freezing in the Credit River (minimum temperature 0.1 °C), West Brook (minimum temperature < 0.0°C), and the experimental stream (winter temperature range 1-2°C) used by Koljonen et al. (2012).

293 This study focused on reach-scale thermal regimes and impacts on trout growth, but
294 smaller groundwater sources could possibly create areas of thermal refugia for trout but not
295 significantly contribute to stream thermal regime. These small groundwater sources could
296 potentially impact trout growth, and use of these temperature refugia by trout at a
297 microhabitat scale may explain some of the variation we observed in brown trout winter
298 growth. Additionally, our estimation of groundwater input at the reach scale may explain some
299 of the possible discrepancies between this study and Cunjak (1996), where brown trout were
300 observed congregating in areas significantly downstream of groundwater input points. Our
301 results suggest that groundwater input can result in favorable thermal conditions on a reach
302 scale for winter growth of brown trout, however additional research into use of groundwater
303 input by brown trout on a microhabitat scale would be beneficial.

304 Juvenile brown trout had faster growth rates than adult brown trout in all study streams
305 except Hay Creek, where adults grew substantially faster than juveniles. A relatively small
306 sample size of adult (6) and juvenile (5) fish and the greater variability in growth observed in
307 Hay Creek relative to the other study streams may have influenced our measures of adult and
308 juvenile growth. Differences in growth rates between juvenile and adult brown trout in this
309 study support similar patterns observed by Dieterman et al. (2012) in three southeast
310 Minnesota streams. The increased growth rate in juvenile fish could have been influenced by a
311 number of factors including habitat suitability, prey availability and sexual maturation
312 (Dieterman et al. 2004; Harvey et al. 2006; Fowler et al. 2009; Jonsson and Jonsson 2011).

Significant decreases in brown trout condition during winter have been found in several studies. For example, trout experienced reduced condition during the winter in the Credit River, despite actively foraging (Cunjak et al. 1987). Kelly-Quinn and Bracken (1990) also noted a decrease in fish condition by the end of winter, particularly in mature (age-1+) brown trout. Cunjak et al. (1987) found that although brook trout continued to feed during the winter, fish condition declined throughout the early winter and remained low until spring. Similarly, Berg and Bremset (1998) found juvenile brown trout had lost up to 70% of their autumn mean fat content by the end of winter in a temperate Norwegian stream. By contrast, brown trout winter condition was significantly associated with the gradient of stream thermal regimes across study streams in this study. Although condition summed across all 24 streams remained stable for juvenile and adult fish from early to late winter, increased thermal stability had a significant positive effect on brown trout condition.

The significant relationship between late winter fish condition, change in overwinter condition and slopes of air-temperature regressions suggests that groundwater input buffered water temperatures sufficiently to allow brown trout to maintain or increase condition during the winter. Conversely, trout in streams with less groundwater input tended to experience reductions in condition, although relatively small sample size in some streams may have affected the explanatory power of the late winter and change over winter regressions ($R^2 = 0.31$ and 0.24 respectively). However, W_r values were calculated from a mean of more than 20 brown trout per stream and variation in W_r was similar between all streams regardless of sample size. Change in winter condition of brown trout was likely influenced by a combination of factors (e.g. habitat availability and trout activity levels) in addition to those examined in this

study. By using the regression equations presented in Fig. 4 to predict fish condition, brown trout in southeastern Minnesota require a stream with an air-water temperature regression slope of ≤ 0.605 (94% of study streams) to maintain a W_r of 80 or higher during winter, and an air-water temperature regression slope of ≤ 0.28 (31% of study streams) to increase condition from early to late winter.

The amount of prey consumed by brown trout did not have a significant impact on growth of juvenile or adult trout. Trout diets regularly contained several hundred prey items during both early and late winter sampling periods, and empty stomachs were rare in all streams, never exceeding 5% of trout sampled in any stream. Similarly, Cunjak and Power (1987), French et al. (2014), and Anderson et al. (2016) all found large numbers of invertebrate prey in brown trout winter diets. Conversely, Kelly-Quinn and Bracken (1990), observed empty stomach rates as high as 15% during winter in the River Dodder (Ireland), suggesting prey availability may vary considerably among streams. Winter aquatic invertebrate abundance is relatively high in groundwater-dominated streams of southeastern Minnesota when compared to streams more heavily influenced by surface water runoff (Nicola and Almodovar 2004; Anderson 2012; Cochran-Biederman 2015), and our data suggest that prey availability is likely not a limiting factor for winter brown trout growth in groundwater-dominated southeastern Minnesota streams.

Prey energy density was not a significant component when modeling winter growth of juvenile or adult brown trout. By contrast, Dieterman et al. (2004) found variation in diet and energy richness of available prey were related to annual growth of brown trout in southeastern

Minnesota streams, as manipulation of diet composition resulted in more accurate predictions of growth by bioenergetics modeling than manipulation of temperature. Differences in analytical methods may have contributed to these differing results, for example, Dieterman et al. (2004) used mean annual cohort growth rate, whereas we used winter growth measured for individual trout in our analyses. Seasonal and individual variation between studies may have differentially influenced estimates of trout growth; thus directly comparing our results to those of Dieterman et al. (2004) is difficult due to the differences in methods. Future research using a bioenergetics approach to investigate the consequences of specific diet composition on winter growth of brown trout could bridge the gaps between our study and Dieterman et al. (2004)

Population density can have a significant effect on brown trout populations, with higher density generally resulting in reduced growth and survival of fish (e.g. Jenkins et al. 1999; Lobón-Cerviá 2007), often through intraspecific competition for food and habitat resources. Although brown trout population densities were not measured in this study, density likely varied between streams and may have impacted winter growth (Carlson et al. 2016). However, southeastern Minnesota streams are productive (Kwak and Waters (1997), and support high density aquatic invertebrate populations (Bouchard and Ferrington 2009; Anderson 2012; Cochran-Biederman 2015; Anderson et al. 2016), which may reduce trout competition for prey. Cochran-Biederman (2015) reported a mean winter benthic invertebrate density of 2,225 individuals*(m²)⁻¹ in 6 southeastern Minnesota streams. Anderson et al. (2016) and Cochran-Biederman (2015) found that brown trout in southeastern Minnesota streams fed heavily on benthic invertebrates during the winter when significant reductions in invertebrate drift were observed. French et al. (2014) and French (2014) observed similar patterns of benthic feeding

by southeastern Minnesota brown trout. Dieterman et al. (2004) found brown trout density was not significantly related to the proportion of maximum consumption predicted from observed brown trout weight gains via bioenergetics modeling. Similarly, neither the quantity nor quality of prey consumed significantly impacted brown trout growth in the 24 streams examined in this study, suggesting brown trout population density likely did not differentially impact winter growth among streams.

Management action to protect groundwater resources would likely benefit trout populations in groundwater-dominated streams. A conservation approach that recognizes the importance of watershed and springshed contributions to water quality in groundwater-dominated streams is required to effectively manage these resources. Accurate mapping of springsheds is a necessary step to understand the hydrology of a specific stream, and will allow managers to make informed decisions on land use practices and groundwater allocations (Green et al. 2002; Williams and Vondracek 2010). Expanding urban areas and changing land use practices (e.g. agricultural tile drainage) will likely place greater demands on current aquifers. Reduced infiltration time for water on the landscape combined with greater human demands from aquifers may result in reduced groundwater flow to streams and lower quality habitat for trout (Zekster et al. 2005; Kløve et al. 2014).

Climate change has the potential to differentially impact groundwater-dominated streams along a thermal stability gradient, i.e. some streams may be more susceptible to warming than others (Krider et al 2013). Direct impacts of increasing air temperature and changes in precipitation, and indirect effects, such as changes in groundwater temperature or

aquifer recharge rates may have important consequences for trout populations (Lyons et al. 2010). Changing climate may lead to shifts in seasonal growth patterns of trout in temperate latitudes, causing seasons with cooler water temperatures, such as winter and early spring to account for a greater proportion of annual growth. Our data may aid managers in identifying streams that are resistant or susceptible to the influence of climate change, thus allowing a more effective distribution of limited resources for trout management activities. For example, resistant streams may be given a higher management priority than susceptible streams that are likely to become less suitable for trout over time.

Thermal stability was the most influential variable in both juvenile and adult growth models, and the addition of a diet variable was not supported for either size group. Reductions of water temperature in winter can have direct and indirect impacts on growth and survival of stream dwelling salmonids. However, groundwater input can effectively buffer water temperatures in winter, creating more stable thermal conditions that benefit trout by increasing prey availability, foraging, growth, and metabolic efficiency. There was a positive relationship between stream thermal stability and brown trout winter growth and condition in this study. Fisheries managers may need to reevaluate the importance of winter when considering management actions on stream trout populations, as significant trout growth can occur in groundwater buffered streams.

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Table 1. Sample dates, the number of marked and recaptured adult and juvenile brown trout used for growth and condition analyses, number of fish tagged, slopes of air-water temperature regressions from Krider et al. (2013) where available, predicted water temperature at -10°C mean weekly air temperature, and maximum stream width for 24 southeastern Minnesota streams sampled for brown trout during the winter of 2010-13. Water temperatures at -10°C were predicted using equations from Krider et al. (2013). NA= not available.

Stream	Early sample date	Late sample date	Fish recaptured: adults, juveniles (fish tagged)	Regression slope	Water temperature at -10°C (C°)	Maximum stream width (m)
Big Springs Creek	12/19/2012	3/22/2013	4,11(67)	0.178	5.80	2.0
Daley Creek	1/6/2011	3/26/2011	8,30(150)	0.204	5.13	3.2
Cold Spring Brook	1/12/2011	3/15/2012	14,7(95)	0.209	4.59	4.8
Trout Valley Creek	12/7/2012	3/7/2013	0,8(24)	0.245	3.65	3.6
Gribben Creek	12/17/2010	3/25/2011	4,24(150)	0.25	4.54	3.5
Torkelson Creek	11/18/2011	2/24/2012	0,21(140)	0.322	3.12	3.4
Winnebago Creek	12/10/2010	3/15/2011	3,7(150)	0.342	3.51	8.5
Garvin Brook	12/5/2010	3/3/2011	3,19(110)	0.345	2.83	15.4
Gilmore Creek	1/7/2012	3/10/2012	4,24(137)	0.347	3.40	3.4
Badger Creek	11/19/2011	3/15/2012	0,19(151)	0.354	3.81	3.7
Hay Creek	12/1/2010	3/30/2011	6,5(150)	0.388	2.58	5.1
South Fork Root River	12/14/2012	3/17/2013	7,5(95)	0.398	2.25	8.5
Beaver Creek	11/19/2010	3/16/2011	0,8(150)	0.443	1.68	9.1
Cedar Valley Creek	12/17/2011	3/3/2012	4,18(136)	0.474	1.25	5.5
East Burns Valley	1/9/2013	3/21/2013	5,0(22)	0.563	0.00	4.2
Pickwick Creek	12/16/2011	3/2/2012	6,18(128)	0.611	0.30	4.3
Upper Money Creek	1/8/2013	3/21/2013	28,15(103)	NA	NA	4.0
Lost Creek	12/14/2012	3/16/2013	5,12(61)	NA	NA	5.8
Camp Creek	12/13/2012	3/16/2013	7,8(139)	NA	NA	7.0
West Beaver Creek	12/18/2012	3/20/2013	5,10(37)	NA	NA	7.5
Bee Creek	12/17/2012	4/3/2013	50,2(136)	NA	NA	5.4
West Albany Creek	12/6/2012	3/6/2013	4,17(105)	NA	NA	7.4
Pleasant Valley Creek	12/7/2012	3/7/2013	7,20(95)	NA	NA	2.5
Spring Creek	12/8/2012	3/8/2013	4,6(22)	NA	NA	11.2

Table 2. Fixed effects for linear mixed effects modeling of winter growth of brown trout. Growth of juvenile (≤ 240 mm TL) and adult (>240 mm TL) fish were modeled separately. Slopes of air-water temperature regressions were obtained from Krider et al. (2013), and prey taxa energy densities from Cummins and Wuycheck (1971).

Variable	Description
Temperature regression	Slope from the temperature regression equation presented in Krider et al. (2013)
Dry weight early	Mean total dry weight of prey consumed in early winter sample
Dry weight late	Mean total dry weight of prey consumed in late winter sample
High energy early	Mean proportion of total dry weight of prey with an energy density >4000 J/g (<i>Gammarus</i> , Ephemeroptera, Plecoptera, <i>Physella</i>) during the early winter sample.
Low energy early	Mean proportion of total dry weight of prey consumed with an energy density <3000 J/g (Diptera, Trichoptera) during the early winter sample.
High energy late	Mean proportion of total dry weight of prey consumed with an energy density >4000 J/g (<i>Gammarus</i> , Ephemeroptera, Plecoptera, <i>Physella</i>) during the late winter sample.
Low energy late	Mean proportion of total dry weight of prey consumed with an energy density <3000 J/g (Diptera, Trichoptera) during the late winter sample.

Table 3. Mixed effects models and selected variables for juvenile and adult brown trout growth ($\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) during the winters of 2010-13. The top three models and the global model are shown. Variables: (a) temperature regression; (b) high energy diets in early winter; (c) low energy diets in early winter; (d) dry weight early winter; (e) high energy late winter; (f) low energy late winter; (g) dry weight late winter. Variables are described in detail in Table 2.

Model	AICc	ΔAICc	AICc Weight
Juvenile			
1. Growth= 3.93 - 7.50(a)	57.98	0.00	0.67
2. Growth= 2.32 - 6.46(a) + 0.02(b)	60.37	2.38	0.20
3. Growth= 3.14 - 7.29(a) + 0.01(e)	61.77	3.79	0.10
4. Growth= 32.56 - 8.88(a) + 0.10(b) + 0.06(c) - 2.14(d) - 0.38(e) -0.35(f) + 1.31(g)	102.71	44.73	0.00
Adult			
1. Growth= 1.34 - 3.72(a)	36.22	0.00	0.82
2. Growth= 1.57 - 3.58(a) - 0.004(b)	40.69	4.47	0.09
3. Growth= 0.87 - 3.36(a) + 0.008(e)	41.02	4.80	0.07
4. Growth= 0.36 - 2.97(a) - 0.001(b) + 0.001(c) - 0.55(d) + 0.008(e) + 0.53(g)	82.43	46.21	0.00

Table 4. Summary information from previous studies examining brown trout winter growth.

Study	Location	Primary thermal regulation	Minimum winter temperature	Mean winter growth rate/change in condition
Dieterman et al. (2012)	Southeastern Minnesota, USA	Groundwater	NA	Growth: 0-0.1 mm/day
French et al. (2014)	Southeastern Minnesota, USA	Groundwater	6.0°C	Growth: 2.55 mg/g/day
Nicola and Almodóvar (2004)	Central Spain	Groundwater and Air	0.5°C	Varied by stream
Watz et al. (2016)	Central Sweden	Groundwater and Air	0.3°C	Growth: SGR 0.1-0.2
Lobón-Cerviá and Rincón (1998)	Galicia, Spain	Air temperature	3.0°C	Growth: 1.4g / Month
Cunjak and Power (1987)	Ontario, Canada	Air temperature	0.1°C	Condition: -0.15 to -0.35
Kelly-Quinn and Bracken (1990)	Leinster, Ireland	Air temperature	mean Jan air temp ~3°C	Negative between Oct and Jan
Carlson et al. (2007)	Massachusetts, USA	Air temperature	0.0°C	Minimal or negative
Koljonen et al. (2012)	Laboratory	NA	1.2°C	Growth: -0.02 to 0.04 g/day
Berg and Bremset (1998)	Trondheim, Norway	Air Temperature	0.0°C	Condition: up to 70 fat loss%

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Figure 1. Map of the Driftless Area of southeastern Minnesota, USA and 24 streams sampled during winters of 2010-13. (1) Hay Creek; (2) Cold Spring Brook; (3) West Albany Creek; (4) Spring Creek; (5) Beaver Creek; (6) Trout Valley Creek; (7) Garvin Brook; (8) Gilmore Creek; (9) East Burns Valley Creek; (10) Pleasant Valley Creek; (11) Cedar Valley Creek; (12) Pickwick Creek; (13) Upper Money Creek; (14) Lost Creek; (15) Torkelson Creek; (16) Big Springs Creek; (17) Daley Creek; (18) Gribben Creek; (19) Badger Creek; (20) Camp Creek; (21) South Fork Root River; (22) West Beaver Creek; (23) Bee Creek; (24) Winnebago Creek.

Figure 2. Mean growth (mg/g/day) of juvenile (≤ 240 mm, A) and adult (> 240 mm, B) brown trout recaptured from streams sampled during winters of 2010-2013. Missing symbols on the far right denote streams where no adult or juvenile fish were recaptured. Error bars = 1 Standard error of the mean.

Figure 3. Mean relative weight (Wr) of pooled juvenile (≤ 240 mm) and adult (>240 mm) brown trout recaptured from streams sampled during winters of 2010-2013. (A) Mean relative weight during early (filled symbols) and late (open symbols) winter for juvenile (circle) and adult (square) trout. (B) Mean change in relative weight between early and late winter. There were no significant differences in mean Wr or change in Wr between age class or time period. N= 315 for juveniles, N= 183 for adults. Error bars = 1 standard error of the mean.

Figure 4. Regressions of mean stream early winter (A), late winter (B), and change overwinter (C) relative weight (Wr) of brown trout against inferred groundwater inputs (Regression slope) in 16 southeastern Minnesota streams during the winters of 2010-2013. Groundwater input increases with slope from 0 to 1. Regression slope is from air/water temperature regressions from Krider et al. (2013). Only significant regressions are shown ($\alpha=0.05$). Error bars = 1 standard error of the mean.