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Brown trout growth in Minnesota streams as related to landscape and local factors

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ABSTRACT

Brown trout (*Salmo trutta*) are ecologically and socioeconomically important throughout the world. As such, understanding population dynamics is critical for brown trout management. Brown trout support a valuable recreational fishery in the Driftless Ecoregion of southeast Minnesota, where growth (i.e. mean back-calculated length-at-age) varies among streams but the relative effects of landscape (i.e. watershed level) and local (i.e. reach-level) factors on growth are unclear. Thus, the objective of this study was to evaluate effects of drainage area on individual brown trout growth relative to the effects of local factors (i.e. thermal regime, riparian land cover, relative abundance) to provide managers with strategies for increasing growth and the abundance of large individuals in southeast Minnesota streams. Linear mixed-effects models with combinations of these factors were compared using information-theoretic model selection and multimodel inference. Age, which explained 63% of variation in growth, differed among streams for age-1 and age-2, but not age-3 brown trout. Model averaging indicated growth of age-1 and age-2 individuals increased primarily with drainage area and secondarily with forested riparian area. Brown trout relative abundance did not affect growth, so it is realistic for managers to sustain high-quality, high-quantity brown trout populations. Overall, this synthetic landscape and local study advances brown trout management by illustrating that systems with large watersheds and forested riparian zones are suitable for management strategies (e.g. harvest regulations, habitat restoration) to increase growth and the abundance of large brown trout in socioeconomically valuable southeast Minnesota streams.

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Growth rate; drainage area; thermal sensitivity; riparian land cover; relative abundance; brown trout

Introduction

Brown trout (*Salmo trutta*) are ecologically and socioeconomically important throughout the world (Budy et al. 2013). Research on individual and population-level growth dynamics of brown trout has occurred at local, regional, national, and international scales across time spans ranging from days to decades (Nicola & Almodóvar 2004; Almodóvar et al. 2006; Logez & Pont 2011; Dodson

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et al. 2013). In the United States, research on brown trout growth (defined herein as mean back-calculated length-at-age, MBLAA) has been widely distributed throughout the western, midwestern, and eastern portions of the country (Wills 2005; Baird et al. 2006; Rasmussen et al. 2011). In the Driftless Ecoregion of southeast Minnesota, stream-dwelling brown trout support an important recreational fishery that provides $1.1 billion in annual economic benefit to local communities (Trout Unlimited 2008). Large brown trout are highly valued by anglers in this region (Vlaming & Fulton 2002; Blann 2004), so it is important to understand factors that influence growth so that fisheries managers can maintain or improve individual growth and thereby sustain or increase the abundance of large brown trout in southeast Minnesota streams.

Brown trout presence/absence, population density, and biomass vary with landscape variables such as surficial geology, catchment area, and land use in southeast Minnesota streams (Blann 2000, 2004; Nerbonne & Vondracek 2001; Zimmerman et al. 2003). In contrast, research on brown trout growth has focused on effects of local factors such as intraspecific density (negative effect on growth in one stream; Newman 1993) and prey availability as mediated by temperature (positive effect on growth in multiple streams; Dieterman et al. 2004). Thus, effects of landscape variables (e.g. drainage area) on growth and their influence relative to local factors (e.g. thermal regime, riparian land cover, brown trout relative abundance) are unanswered research questions.

Relative to smaller streams, those with larger drainage area have greater habitat volume (Jonsson et al. 2001; Parra et al. 2009) and secondary production (Arismendi et al. 2012), conditions that may increase brown trout growth in southeast Minnesota streams. In addition, groundwater input decreases stream thermal sensitivity (i.e. relative susceptibility to temperature change) by buffering cold winter and warm summer temperatures (Nicola & Almodóvar 2004; Krider et al. 2013), which may augment growth by increasing prey availability (Dieterman et al. 2004) and foraging efficiency (Elliott et al. 1995). In southeast Minnesota streams, brown trout biomass increases with forested riparian area and decreases with cultivated and grassland riparian area (Blann 2000, 2004). The mechanisms by which forest vegetation promotes brown trout biomass production (e.g. increased prey availability and woody habitat, decreased temperature due to shading, reduced sediment erosion and nutrient enrichment; Baxter et al. 2005; Vondracek et al. 2005) may also increase growth.

The objective of this study was to evaluate effects of a landscape variable (i.e. drainage area) on individual brown trout growth relative to the effects of local factors (i.e. thermal regime, riparian land cover, brown trout relative abundance) to provide managers with new information relevant for increasing growth and the abundance of large brown trout in socioeconomically valuable southeast Minnesota streams. We hypothesized that brown trout growth varies among streams in proportion to drainage area because habitat volume, water temperature, and prey availability generally increase with watershed size (Jonsson et al. 2001; Arismendi et al. 2012). We predicted that growth is negatively associated with thermal sensitivity as relatively warm summer and cool winter temperatures in thermally sensitive streams are less favorable for growth than stable temperatures in systems with groundwater-driven thermal buffering (Elliott et al. 1995; Dieterman et al. 2004). Moreover, we expected that growth would follow patterns in brown trout biomass and thus increase with forested riparian area and decrease with cultivated and grassland riparian area (Blann 2000, 2004). Finally, we hypothesized that growth is not associated with brown trout relative abundance due to exceptionally high productivity and prey availability in southeast Minnesota streams (Dieterman et al. 2012).

Methods

The study occurred in the Driftless Ecoregion of southeast Minnesota, USA. This region remained unglaciated during the most recent Wisconsin glaciation and was characterized by numerous valleys, wooded slopes, and prairie bluffs punctuated by row-crop (e.g. corn, soybean) agricultural fields on hilltops and valley bottoms (Vondracek et al. 2005). Dominant land cover types in the study region were, in descending order, row-crop agriculture, forest, grassland/pasture, and urban (Blann 2000, 2004).

Figure 1. University of Minnesota researchers B. Vondracek (right) and W. E. French sampling brown trout in the Driftless Ecoregion of southeast Minnesota.
Image courtesy of University of Minnesota Conservation Biology Graduate Program.

Brown trout were collected from 150-m reaches in seven streams in winter 2010−2011 using a backpack electrofisher (LR 20B, Smith Root, Inc.; http://smith-root.com; Figure 1). Sampling occurred in groundwater-dominated streams (i.e. groundwater-driven thermal buffering was sufficient to prevent over-winter freezing) during three time periods (November−December 2011, January−February 2011, and March−April 2011). Sampling spanned an array of habitats (pools, riffles, runs) so that brown trout could be collected across an age range conducive for growth analysis. In each stream, total length and mass of age 1−3 fish ($\leq$ 150 individuals) were measured and a random subset (52−82 individuals) was selected for growth analyses (Table 1). Four to eight scales were removed from the left posterior dorsal region of each individual and mounted on microscope slides with cover slips and Permount™ glue. Mounts were magnified on a microfiche reader, photographed, and assessed using digital age and growth software (Fish BC 3.0). Ageing and growth analysis occurred along the longest axis of the highest resolution scale. Age correspondence between two independent readers was >90%.

Growth (MBLAA) was calculated for each stream using the Fraser−Lee method (Quist et al. 2013):

$$L_i = S_i{}^*[(L_c - a)/S_c] + a$$

where S_c is the scale radius at capture, L_c is the fish length at capture, S_i is the scale radius at time i, L_i is the fish length at time i, and a is the intercept of the scale radius−fish length regression equation (i.e. 10; Ojanguren & Braña 2003). Brown trout growth metrics (MBLAA-1, MBLAA-2, and MBLAA-3 for ages 1, 2, and 3, respectively) were tested for normality and homoscedasticity in program R (version 2.13.2; R Development Core Team 2013) and compared among streams using one-way analysis of variance (ANOVA) with a *post hoc* Tukey's Honestly Significant Difference (HSD) test.

Drainage area for each stream was measured using the United States Geological Survey StreamStats interactive map application (USGS 2015; Table 2). Thermal sensitivity was expressed as the

Table 1. Brown trout sampling information (UTM coordinates; elevation (m); number of age-1, age-2, and age-3 individuals) and growth metrics (mean back-calculated length-at-age-1 (MBLAA-1), age-2 (MBLAA-1), and age-3 (MBLAA-3)) in southeast Minnesota streams.

Stream	UTM	Elevation	Age-1	Age-2	Age-3	MBLAA-1	MBLAA-2	MBLAA-3
Beaver	577,026, 4,889,127	219.9	52	16	12	126.0 (2.4)[d]	201.6 (3.2)[d]	266.3 (2.8)
Forestville	561,631, 4,831,893	324.8	28	13	39	144.8 (3.8)[a,b]	228.7 (3.7)[a,b,c]	278.7 (4.3)
Gribben	587,631, 4,839,986	262.8	39	38	4	129.6 (2.6)[c,d]	203.1 (3.8)[d]	281 (14.1)
Hay	532,802, 4,925,099	259.0	30	18	4	140 (3.2)[a,b,c]	215.6 (3.9)[c]	279 (5.5)
MBW	572,079, 4,876,366	304.1	24	13	20	132.1 (4.3)[b,c,d]	238.1 (5.2)[a,b]	284.8 (7.7)
SBW	581,763, 4,880,221	235.9	38	18	26	149.3 (3.5)[a]	239.5 (3.7)[a]	289.6 (5.5)
Winnebago	625,126, 4,823,555	239.9	42	31	7	123.4 (3.5)[d]	220.3 (6.3)[b,c]	304.5 (7.6)

Note: Different letters (a, b, c, and d) denote significant differences (Tukey's Honestly Significant Difference test, $p < 0.05$) among streams within growth metric categories (e.g. MBLAA-1, MBLAA-2). MBW = Middle Branch Whitewater, SBW = South Branch Whitewater.

Table 2. Landscape and local factors in southeast Minnesota streams.

Stream	Area	TS	% forested	% grassland	% cultivated	RA
Beaver	29.1	0.44	10	85	5	90
Forestville	41.9	0.21	55	43	2	49
Gribben	20.4	0.25	45	45	10	151
Hay	54.6	0.39	15	35	50	80
Middle Branch Whitewater	78.2	0.52	15	45	40	44
South Branch Whitewater	202.1	0.50	35	50	15	80
Winnebago	61.6	0.34	13	82	5	98

Note: Area = drainage area (km^2), TS = thermal sensitivity (air−water temperature regression slope), % forested = forested riparian percentage, % grassland = grassland riparian percentage, % cultivated = cultivated riparian percentage, and RA = brown trout relative abundance (individuals per hour).

slope of air−water temperature regressions developed in a companion study (Krider et al. 2013) using 1998−2009 air temperatures and 2007−2009 water temperatures (Table 2). Slopes closer to one indicated higher thermal sensitivity (i.e. lower groundwater input) and a greater effect of air temperature on water temperature, and vice versa. Two-way ANOVA was used to test whether air−water temperature regression slopes were more variable among streams than among years and thus reliable indices of thermal sensitivity. Riparian land cover (% forested, % grassland, % cultivated) was measured on both sides of each stream reach using the 2011 National Land Cover Database in ArcMap 10.2 (Table 2). Riparian zone width was defined as 100 m to be consistent with previous stream research in southeast Minnesota (Vondracek et al. 2005). Forested land cover included areas where trees were >5 m tall and comprised >20% of total vegetation cover (NLCD 2015). Grassland land cover included areas in which graminoid or herbaceous vegetation comprised >80% of total vegetation cover. Cultivated land cover encompassed agricultural areas used for production of corn and/or soybeans that comprised >20% of total vegetation cover. Brown trout relative abundance (i.e. catch per unit effort, individuals per hour; Table 2) in November 2010 was used as a density index because single-pass electrofishing (rather than multi-pass depletion sampling) was conducted.

Linear mixed-effects models were developed to determine which landscape and/or local factors explained among-stream variation in brown trout growth. Specifically, random intercept and slope models (Zurr et al. 2009) were constructed to assess the relative influence of drainage area (Area), thermal sensitivity (TS), riparian land cover (% forested (For), % grassland (Grass), % cultivated (Cult)) and brown trout relative abundance (RA) on growth of age classes that exhibited among-stream variation in MBLAA. Model intercepts were allowed to vary by age and slopes to vary by stream (including Area as a random effect was analogous to modeling among-stream differences in growth). For all predictor variables, fitted versus residual plots and qqnorm plots were created in program R to evaluate assumptions of normality and homoscedasticity, and predictors were ln-

Table 3. Results of linear mixed-effects modeling to explain variation in brown trout growth among southeast Minnesota streams as a function of stream drainage area (Area, km^2), stream thermal sensitivity (TS, air–water temperature regression slope), % forested riparian area (For), % grassland riparian area (Grass), % cultivated riparian area (Cult) and brown trout relative abundance (RA, individuals per hour).

Model	N	K	AIC	AICc	ΔAICc	w_i
Growth = Area + For + RA + (1 + Area|Age)	7	5	10,323.79	10,323.92	0.00	0.46
Growth = Area + For + Grass + RA + (1 + Area|Age)	7	6	10,325.24	10,325.41	1.49	0.22
Growth = Area + Grass + RA + (1 + Area|Age)	7	5	10,326.34	10,326.47	2.55	0.13
Growth = Area + TS + Grass + (1 + Area|Age)	7	5	10327.85	10327.99	4.07	0.06
Growth = Area * RA + For + (1 + Area|Age)	7	4	10,329.22	10,329.38	5.46	0.03
Growth = Area + TS + Grass + RA + (1 + Area|Age)	7	6	10,329.40	10,329.57	5.65	0.03
Growth = Area * RA + For + Grass + (1+Area|Age)	7	5	10,329.84	10,330.05	6.13	0.02
Growth = Area * RA + Grass + (1 + Area|Age)	7	4	10,330.95	10,331.12	7.20	0.01
Growth = Area + TS + RA + (1 + Area|Age)	7	5	10,331.53	10,331.66	7.74	0.01
Growth = Area + TS + For + RA + (1 + Area|Age)	7	6	10,331.78	10331.95	8.03	0.01
Growth = Area + TS + (1 + Area|Age)	7	4	10,331.92	10,332.03	8.11	0.01
Growth = Area + TS + For + Grass + (1+Area|Age)	7	6	10,332.02	10,332.19	8.27	0.01
Growth = Area + TS + For + Grass + RA + (1+Area|Age)	7	7	10,333.01	10,333.22	9.30	0.00
Growth = Area + TS + For + Grass + Cult + RA + (1 + Area|Age)	7	8	10,333.01	10,333.22	9.30	0.00
Growth = Area + RA + (1 + Area|Age)	7	4	10,337.36	10,337.47	13.55	0.00

Note: N = sample size (number of streams); K = number of parameters (fixed effects plus intercept and error); AIC = Akaike's information criterion; AICc = AIC corrected for small sample size; ΔAICc = difference in AICc between each model and the most supported model; w_i = Akaike weight (relative strength of evidence for each model).

transformed where appropriate. All models followed the basic form of the global model with associated assumptions (Zurr et al. 2009):

$$\text{Growth}_i = \alpha_i + \text{Area}_i + \text{TS}_i + \text{RA}_i + \text{For}_i + \text{Grass}_i + \text{Cult}_i + (1 + \text{Area}_i \mid \text{Age}_i) + \varepsilon_i \quad (1)$$
$$b_i = N(0, D_b)$$
$$\varepsilon_i = N(0, D_\varepsilon)$$
$$b_1, \ldots, b_n, \varepsilon_1, \ldots, \varepsilon_n, \text{ independent}$$

where α represents the model intercept and ε denotes the model error in each individual stream i. The first assumption was that the random effects b_i were normally distributed with mean 0 and variance D_b. The second assumption was that the errors ε_i were normally distributed with mean 0 and variance D_ε. The third assumption was that b_i and ε_i were independent.

A priori models (n = 15; Table 3) were developed as biologically driven working hypotheses (Chamberlain 1965) regarding effects of landscape and local factors, as well as their interactions, on brown trout growth (see Introduction). All 15 models represented permutations of ≥2 of these hypotheses. Using an information-theoretic approach, models were compared with Akaike's information criterion corrected for small sample size (AICc; Burnham & Anderson 2002) calculated in program R. Full-model averaging (Lukacs et al. 2009) was performed on models with $\Delta_i \leq 2$ (i.e. within two AICc units of the most parsimonious model) to make robust inferences from all informative models (i.e. multimodel inference; Burnham & Anderson 2002).

Results

Growth varied among streams for age-1 ($F_{7,\,544} = 8.66$; $p < 0.01$) and age-2 ($F_{7,\,361} = 12.57$; $p < 0.01$), but not age-3 ($F_{6,\,109} = 2.06$; $p = 0.07$) brown trout (Table 1). MBLAA-1 was the highest (149.3 mm) in the South Branch of the Whitewater River (SWW) and the lowest in Winnebago Creek (123.4 mm, 17.3% smaller) and Beaver Creek (126.0 mm, 15.6% smaller; Table 1). MBLAA-2 was the highest (239.5 mm) in SWW and the lowest in Beaver Creek (201.6 mm, 15.8% smaller) and Gribben Creek (203.1 mm, 15.2% smaller). Air–water temperature regression slopes were

Table 4. Intercepts and coefficients for the two most parsimonious linear mixed-effects models and the model-averaged estimator to explain variation in brown trout growth among southeast Minnesota streams.

Model	w_i	Age	Intercept	Area	For	Grass	RA
Growth = Area + For + RA + (1 + Area|Age)	0.46	1	110.6	6.61	0.23	–	−0.09
		2	162.7	14.77	0.23	–	−0.09
		Global	136.6	10.69	0.23	–	−0.09
Growth = Area + For + Grass + RA + (1 + Area|Age)	0.22	1	119.9	6.23	0.16	−0.12	−0.08
		2	172.5	14.26	0.16	−0.12	−0.08
		Global	146.2	10.25	0.16	−0.12	−0.08
Model-averaged		1	76.9	4.39	0.14	−0.03	−1.08
		2	112.3	9.89	0.14	−0.03	−0.06
		Global	94.6	7.14	0.14	−0.03	−0.06

Note: w_i = Akaike weight (relative strength of evidence for each model).

reliable indices of stream thermal sensitivity as they varied significantly among streams ($F_{6,\ 22}$ = 16.43; $p < 0.01$) but not among years within streams ($F_{1,\ 22} = 0.01$; $p = 0.91$).

Linear mixed-effects modeling indicated that brown trout age explained the greatest percentage (63%) of spatial variation in growth. A model including drainage area, forested riparian area, and brown trout relative abundance was most supported (Akaike weight (w_i) = 0.46; Table 3). An alternative model including these factors plus grassland riparian area was also supported (Δ_i = 1.49; w_i = 0.22; Table 3). For age-1 and age-2 brown trout, individual models and the model-averaged estimator included a large growth effect of drainage area (+); small effects of forested riparian area (+), grassland riparian area (−), and relative abundance (−); and no effect of cultivated riparian area (Table 4). The positive association between drainage area and growth was stronger for age-2 than age-1 brown trout (Table 4).

Discussion

Brown trout growth was most influenced by age, followed by a landscape variable (drainage area) and a local factor (forested riparian area). Growth declined with age as younger, smaller brown trout have a greater scope for growth and invest more energy in production of somatic tissue than older, larger individuals. In addition, growth increased with drainage area, as documented in previous studies (Jonsson et al. 2001; Lobon-Cervia 2003, 2005; Dieterman et al. 2006; Parra et al. 2009). The mechanism for this association may relate to spatial heterogeneity in brown trout age and size at maturity (L'Abée-Lund et al. 1989; Olsen & Vollestad 2005). Drainage area influences local factors (e.g. habitat volume, prey availability) that drive differential opportunity for growth in large or higher opportunity systems and small or lower opportunity systems. It is likely that brown trout in smaller streams with lower habitat volume and prey availability matured earlier than individuals in larger systems that delayed maturation and continued growing amidst high-opportunity conditions.

Results from this study also indicate that forested riparian areas promote small increases in brown trout growth compared to grassland and cultivated riparian areas in southeast Minnesota streams. Wooded vegetation provides habitat (woody debris), mediates temperature, stabilizes stream banks, reduces sedimentation, and delivers inputs of terrestrial invertebrates (Montgomery 1997; Lyons et al. 2000; Blann et al. 2002; Baxter et al. 2005), mechanisms that likely augmented brown trout growth. In contrast, brown trout relative abundance, grassland and cultivated riparian area, and thermal sensitivity had minor or nonexistent effects on growth. This supports conclusions reached by Dieterman et al. (2012), who noted that limestone bedrock geology and agricultural watersheds promote high productivity in southeast Minnesota streams such that typical brown trout growth factors like prey availability, intraspecific density, social dominance are less important than in other regions (Bohlin et al. 2002; Kaspersson & Hojeso 2009). Although thermal sensitivity did not explain spatial variation in an annual index of growth (MBLAA), previous research indicated late-winter brown trout condition (relative weight; Neumann et al. 2013) was positively associated with groundwater input and negatively associated with thermal sensitivity in southeast Minnesota streams (French 2014; French et al. 2014). Thus, the effect of thermal sensitivity on growth may be the strongest in cold winter conditions. Fisheries managers can expect brown trout length to increase primarily with drainage area and secondarily with forested riparian area. Moreover, it is realistic for managers to sustain high-quality, high-quantity brown trout populations in the socio-economically valuable southeast Minnesota streams studied herein because growth is not affected by relative abundance. Thus, management strategies to increase growth and the abundance of large brown trout (harvest regulations, habitat restoration) should be prioritized in larger, more forested streams and need not account for density-dependent growth.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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