

RESEARCH ARTICLE

Population dynamics of brown trout in a Minnesota (USA) stream: A 25-year study

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Abstract

Brown trout (*Salmo trutta*) were surveyed by mark recapture in a 200-m section of Gilmore Creek, Minnesota, annually during fall 1989–2013 to assess long-term trends in abundance. Young-of-year (YOY) fish comprised >68% of the population annually, but age 3 and older fish were present in 23 of 25 years. Trout abundance varied irregularly, peaking every 4 to 6 years. Fall densities of YOY brown trout were positively correlated with median annual stream discharge but inversely correlated with 10% exceedance discharge in May, at a nearby gaged stream. Changes in brown trout abundances were synchronized with those of trout in 2 nearby streams. Annual mortality rates (mean = 74%) and sizes of YOY trout were correlated with YOY densities, with high densities (>1.0 fish/m²) producing small size during fall and high cohort mortality. High YOY densities resulted in low proportional size structure-quality (PSS_Q, <20%) 1 and 2 years later. If similar brown trout population dynamics occur in other streams within the region, interpretation of short-term studies of brown trout (e.g., regulation evaluations, creel surveys, population response to habitat improvement, seasonal movements, and growth rates) may be confounded.

KEYWORDS

brown trout, density dependence, hydrology, mortality, population dynamics

1 | INTRODUCTION

The brown trout (*Salmo trutta*) has played an important role in coldwater streams and rivers in the United States since its introduction from Europe. Hatchery-sustained and naturalized populations throughout the U.S. support fisheries that contribute millions of dollars to local and regional economies (Hart, 2008). So that stream populations of brown trout for angling can be managed better, population dynamics of the species have been examined under varying conditions (e.g., Dieterman, Hoxmeier, & Staples, 2012; Zorn & Nuhfer, 2007a, 2007b). Brown trout population dynamics often are best examined through long-term studies, especially those of a duration sufficient to span multiple, complete life cycles (Elliott, 1994; Waters, 1999). However, such long-term (10–40+ years) studies are relatively rare in the United States (Carline, 2006; Jenkins, Diehl, Kratz, & Cooper, 1999; Warren, Ernst, & Baldigo, 2009; Waters, 1999; Zorn & Nuhfer, 2007a, 2007b) and Europe (Almodóvar, Nicola, Ayllón, & Elvira, 2012; Alonso, García de Jalón, Álvarez, & Gortázar, 2011; Cattaneo, Hugué, & Lamouroux, 2003; Elliott, 1993; Lobón-Cerviá, 2007b). Long-term studies have provided insight on brown trout dynamics that could not be gathered in shorter periods, such as invasion and species

replacement (Waters, 1999), regional, synchronized climatic (hydrologic) control of recruitment (Alonso et al., 2011; Carline, 2006; Cattaneo et al., 2003; Zorn & Nuhfer, 2007b), and density-dependent growth (Jenkins et al., 1999; Lobón-Cerviá, 2007a; Zorn & Nuhfer, 2007a) and mortality (Lobón-Cerviá, 2012; Lobón-Cerviá, Buday, & Mortensen, 2012; Zorn & Nuhfer, 2007a).

The coldwater stream fisheries of southeastern Minnesota, USA, have been managed for 140 years, with brown trout as a major component of most streams for more than a century (Thorn, Anderson, Lorenzen, Hendrickson, & Wagner, 1997). These spring-fed streams support some of the highest production of stream-dwelling salmonids in the country (Kwak & Waters, 1997) because the region's karst geology produces aquifers with high alkalinity (Waters, 1977). Studies have investigated trout populations within the region (e.g., Dieterman, Thorn, & Anderson, 2004; Dieterman, Thorn, Anderson, & Weiss, 2006; Dieterman et al., 2012), but none have been long term, making it difficult to separate the effects of rare events on population dynamics from real trends (Waters, 1999). Lack of information on growth and other population parameters hinders current brown trout management efforts and may limit our ability to predict the effects of anthropogenic changes (Dieterman et al., 2012; Jensen et al., 2008). The objective of

this study was to use data gathered during a 25-year period at a single stream site in southeastern Minnesota to investigate the population dynamics of brown trout. By surveying brown trout in the same 200-m stream reach during the same period each fall, trends in abundance, biomass, growth, mortality, and size structure, and their potential links with hydrology could be examined over a period spanning approximately six generations (3- to 4-year life span typical for this region; Dieterman & Hoxmeier, 2011).

2 | METHODS

2.1 | Study site

Gilmore Creek is a first- to second-order coldwater stream in the Driftless Area Ecoregion of southeastern Minnesota, USA. It is a small (8-km stream length) tributary of the Mississippi River, draining a 26-km² watershed (52% forest/shrub, 30% pastureland, 12% developed, 5% cropland, and 1% other).

The study site (44°01'44"N, 91°42'15"W) on Gilmore Creek was 200 m in length (44 X mean stream width), similar in length or longer than reaches used in long-term studies of brown trout (Lobón-Cerviá, 2012; Lobón-Cerviá et al., 2012; Zorn & Nuhfer, 2007a). The study section was shallow (mean depth = 25 cm) and slow flowing (mean current velocity = 15 cm/s), with low but stable discharge (0.10 m³/s) from nearby springs and a water surface area of approximately 0.1 ha. Stream habitat types were well balanced (28% riffle, 39% run, and 33% pool), and substrates were heterogeneous (3% boulder, 10% cobble, 31% gravel, 25% sand, and 31% silt). Cover for trout (deep [>30 cm] water, cover logs, and submerged macrophytes) encompassed 54% of total stream area. Midday water temperatures typically were 14–17°C in summer, 2–4°C in winter, and 10–13°C during fish surveys in fall.

Gilmore Creek has been managed (via trout stocking, stream habitat improvement, and angling regulations) as a coldwater trout stream for over a century. Brown trout were introduced into the stream prior to 1906 (S. Klotz, MN DNR, personal communication), and yearling fish were stocked annually from 1957 through 1973. Stocking was discontinued after 1973 when the population became self-sustaining (D. Dieterman, MN DNR, personal communication). Brown trout and slimy sculpin (*Cottus cognatus*) were the only fish species present in the study reach. The stream is open to angling, but public access is limited and the trout population is essentially unexploited.

Two additional, 200-m-long stream sites, one site 2.5 km downstream on Gilmore Creek at Saint Mary's University (Gilmore Creek-SMU) and another site 9 km east on Pleasant Valley Creek, also were examined for trout abundance during 2003–2013. Both sites were similar to the main Gilmore Creek study reach in their physical characteristics (mean width = 4.2–4.7 m, surface area < 0.1 ha, discharge = 0.05–0.15 m³/s), fish communities (dominated by brown trout, few slimy sculpin, or other species), and access (private property and essentially unexploited fisheries).

2.2 | Fish collections

Brown trout populations were assessed with a two-sample, mark-recapture design every autumn, 1989 through 2013, during a 2-week

period in late September and early October (preceding spawning by 2 to 3 weeks). A multiyear tagging study (Dieterman & Hoxmeier, 2011) demonstrated that adult brown trout in similar area streams were sedentary, using the same stream section for summer feeding, fall spawning, and overwintering.

Brown trout were captured each fall with a backpack electrofisher (Smith-Root Type VII, Model 12-B POW, or LR-24). Fish were measured for total length (cm), marked temporarily by removal of the caudal fin tip, and released at the site of capture. One week after marking, trout again were collected from the same reach, measured, and recorded as marked (recapture) or unmarked. No dead, marked fish were observed during recapture dates, so mortality due to handling and marking was assumed to be negligible. Scales were collected from 10% to 15% of fish for age determination, and fish were returned to the stream. During several years, trout spanning the complete size range of fish collected during the recapture sampling run were measured (mm total length) and weighed (0.1 g wet weight, Ohaus Model CT1200 portable scale) to determine the length–weight relationship (Ney, 1999). The same collection procedures were followed at the two additional stream sites from 2003 to 2013.

2.3 | Stream hydrology

Gilmore Creek and other nearby streams either lacked active gaging stations or had incomplete flow histories, so daily stream discharge data from the Black River near Galesville, Wisconsin (USGS Water Data website, gage 05382000; 33 km from Gilmore Creek) were used to represent regional stream hydrology for the entire study period. Previous studies (Cattanéo et al., 2003; Lobón-Cerviá, 2007b; Zorn & Nuhfer, 2007a, 2007b) demonstrated the synchrony of stream hydrologies across broad geographic areas. Discharge data were summarized (e.g., mean and median annual discharge, mean, median, and Q_{10} [10% exceedance] discharges for the months of March, April, and May) to assess possible relationships with trout recruitment (Carline, 2006; Cattanéo et al., 2003; Lobón-Cerviá & Rincón, 2004; Lobón-Cerviá et al., 2012).

2.4 | Data analyses

The Bailey modification of the Peterson mark-recapture method (Krebs, 1989) was used to estimate total trout abundance each year. This closed-population method was used instead of an open-population approach because of (a) the single mark and recapture periods, (b) the short time interval (7 days) between marking and recapture, and (c) the low rate of movement of brown trout during this season in similar area streams (Dieterman & Hoxmeier, 2011). Length–frequency plots and scale analyses delineated age groups, and abundance estimates were calculated for each age group present within the stream reach.

Brown trout length–frequency distributions each year were used to calculate proportional size structure (PSS) indices (Neumann & Allen, 2007). Various PSS measures (number of fish of specified length or greater divided by the number of fish of stock length, expressed as a percentage; Neumann & Allen, 2007) assessed changes in population size structure throughout the study period. Total length size categories used for brown trout PSS were stock (≥ 15 cm), quality (≥ 23 cm [PSS_Q]),

preferred (≥ 30 cm [PSS_P]), memorable (≥ 38 cm [PSS_M]), and trophy (≥ 46 cm [PSS_T]; Milewski & Brown, 1994).

Yearly age-group abundances were used to estimate annual mortality rates for brown trout. Mortality rates were calculated via a modification of the catch curve analysis method, using abundances of the same cohort through the years (Miranda & Bettoli, 2007).

Temporal trends across the study period were assessed for trout abundance (total and age-group), densities, standing crop biomass, mortality rates, and PSS_Q using simple time series analyses (Zar, 1984). Traditional stock-recruitment models (Maceina & Pereira, 2007) were developed and compared to examine the influence of adult abundance on the abundance of age 0 fish. Abundance estimates also were used to calculate per capita rate of change ($r = \ln[N_t/N_{t-1}]$) for the entire population and its various subcomponents (Age 0 = young-of-year [YOY], Age 1 = yearling, and Age 2+ = adults) to examine population dynamics throughout the study period (Grossman, Nuhfer, Zorn, Sundin, & Alexander, 2012).

Simple models helped assess the influence of trout density (total and age group) on (a) per capita rate of increase of the entire population and various age groups, (b) mean fall size of age 0 fish, (c) cohort mortality rates, and (d) PSS_Q. Additional models examined the influence of various stream discharge measures on fall densities of age 0 fish, and the relationship between cohort mortality rates and PSS_Q. Predictive

relationships were examined with linear regression, and explanatory power of competing models was compared using Akaike's information criterion for small sample sizes (AIC_c; Brown & Guy, 2007; Burnham & Anderson, 2002). Only those explanatory models with Akaike weights (w_i) $\geq 10\%$ of the w_i of the best model were interpreted. Explanatory powers of competing models were calculated by dividing the w_i value of the best model by that of the competing model. Regression analyses and model comparisons were conducted with JMP Pro (SAS Institute Inc, 2015) or VassarStats statistical software (VassarStats: Website for Statistical Computation; www.vassarstats.net).

3 | RESULTS

3.1 | Population assessments and dynamics

Over 7,800 brown trout were captured during the 25 fall surveys (total length range = 5–56 cm). Fish typically represented four age groups (ages 0–3), with older fish (ages 4–8) usually rare (<1% of total catch) within the study reach. For all years combined, age 0 trout comprised >68% of the total catch.

Abundance estimates varied sixfold during the 25 years (Table 1). Fish abundances changed irregularly over 4- to 6-year intervals throughout the study (Table 1, Figure 1), but time series analyses did

TABLE 1 Population parameters calculated for brown trout each fall 1989–2013 for a 200-m section of Gilmore Creek, southeastern Minnesota

Year	Number of fish marked	Recapture rate (%)	Total population estimate (SE)	Density (fish/m ²)	Annual mortality rate (%)	PSS _Q (%)
1989	87	23.0	522 (102)	0.37	—	—
1990	169	47.3	374 (31)	0.45	75.0	41.4
1991	143	16.8	1121 (205)	0.93	82.1	47.2
1992	228	28.9	779 (79)	0.72	77.6	16.5
1993	237	20.7	630 (70)	0.59	69.5	21.7
1994	243	20.6	648 (71)	0.61	81.5	20.7
1995	369	33.3	1283 (97)	1.08	86.8	25.3
1996	300	18.0	933 (103)	1.29	73.1	26.4
1997	179	20.1	1698 (261)	1.79	83.2	5.9
1998	176	14.8	1682 (301)	2.06	88.9	20.1
1999	94	20.2	432 (83)	0.61	67.1	0.0
2000	213	45.1	430 (31)	0.48	75.2	11.0
2001	221	33.5	633 (59)	0.81	76.6	29.4
2002	243	25.1	996 (109)	1.08	83.9	18.4
2003	169	32.0	381 (38)	0.45	62.6	29.2
2004	136	41.2	322 (32)	0.40	71.2	22.5
2005	127	41.7	299 (31)	0.37	55.2	44.0
2006	180	22.8	535 (67)	0.61	70.8	22.2
2007	77	36.4	268 (41)	0.30	50.9	28.0
2008	97	35.1	258 (34)	0.25	56.7	52.9
2009	207	42.0	630 (55)	0.59	62.9	57.7
2010	209	29.7	1022 (114)	0.93	76.5	18.9
2011	229	37.1	676 (59)	0.65	—	33.0
2012	273	38.5	598 (43)	0.53	—	33.3
2013	229	41.5	408 (27)	0.44	—	25.0
Mean (SD)	193 (70)	30.6 (9.8)	702 (405)	0.75 (0.45)	72.7 (10.5)	27.1 (13.9)

Note. PSS_Q = proportional size structure-quality.

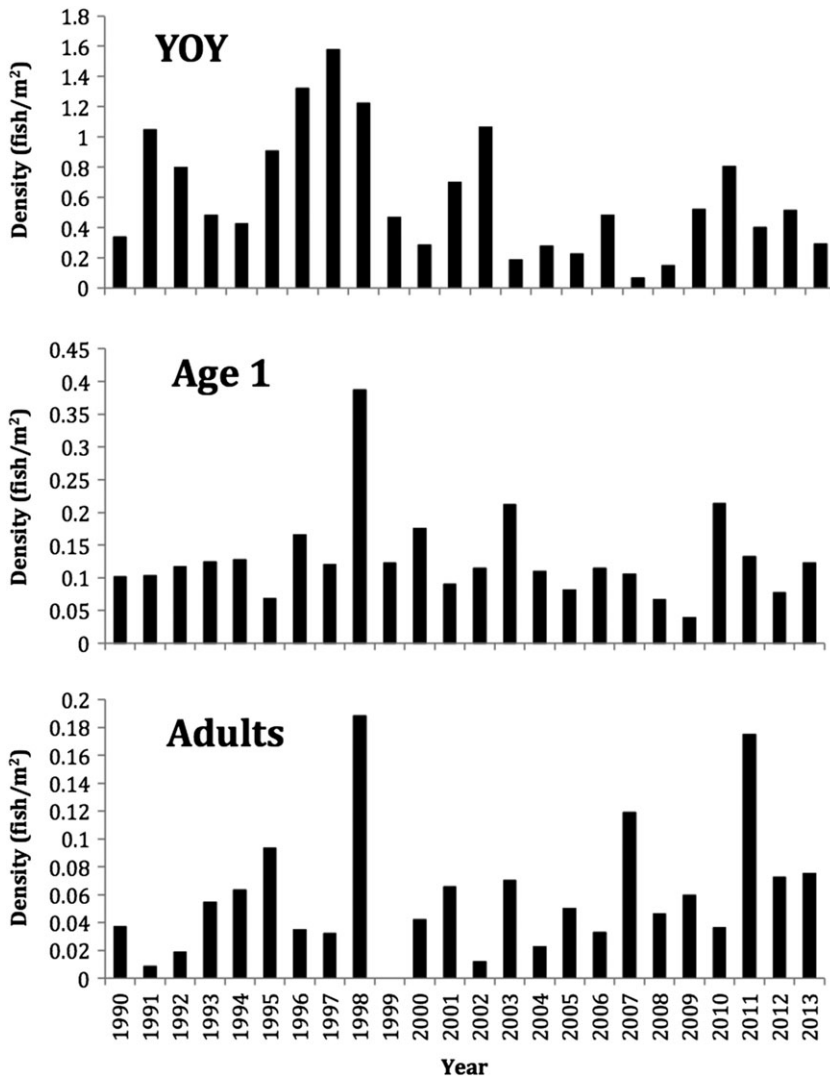


FIGURE 1 Abundance estimates for three age classes of brown trout for a 200-m study reach of Gilmore Creek based on mark-recapture studies, September–October 1990–2013. YOY = age 0 fish; Adult = ages 2, 3, and older fish

not detect the presence of a significant cycle of any period among the 25 years. There also was no significant (simple linear regression: $t(23) = 1.49, p = .16, r^2 = .08$) long-term trend in total abundances during the study period. Abundance changes and peak densities at the main study site were synchronized with those at two additional, nearby stream sites examined since 2003 (Figure 2). Trout densities were correlated significantly (Pearson correlations 0.534–0.824, all $p < .05$) between all site pairs, with all sites achieving peak densities simultaneously in 2006 and 2010.

Comparisons of abundances between age groups in different years produced only a single, significant relationship (simple linear regression: age 1 density [fish/m²] during year $t = 0.114 * [\text{age 0 density (fish/m}^2\text{) during year } t + 1] + 0.0594; t(21) = 4.04, p = .0006, r^2 = .44$). Comparisons of densities between older age groups, between age 0 fish 1 year and adults 2 and 3 years later, and between potential spawning-age fish 1 year and age 0 fish the following year were all not significant (all $p > .4$). A Ricker stock-recruitment model developed for spawning-age (age 2 and older) and age 0 fish was a better fit than a Beverton–Holt model, but even in the Ricker model, spawning-age density in year t explained only 5% of the variability in age 0 density in year $t + 1$.

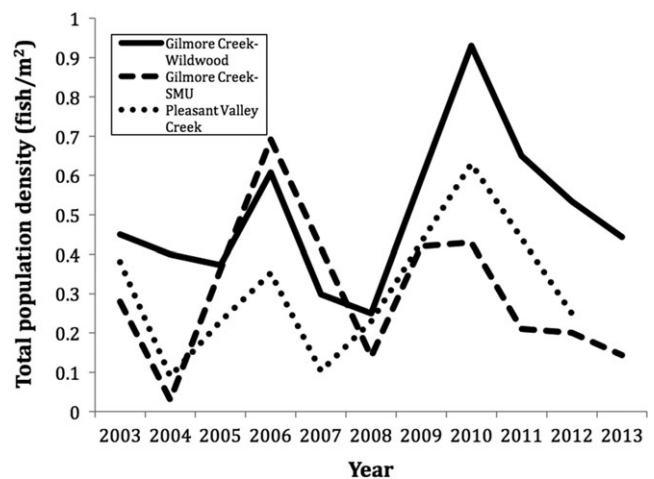


FIGURE 2 Total densities of brown trout at three stream sites (Gilmore Creek at Wildwood Drive, Gilmore Creek at Saint Mary's University [SMU], and Pleasant Valley Creek at Valley View Estates) in and near Winona, Minnesota, based on total population estimates from annual mark-recapture studies, September–October 2003–2013

Density of age 0 (YOY) brown trout had strong explanatory power on per capita rate of change for the entire population in the 200-m reach (Table 2, Figure 3). Models including either yearling or adult fish were 12.8 and 16.6 times less likely, respectively, than the YOY model in explaining per capita rate of change of the entire population.

TABLE 2 Candidate simple models for the Gilmore Creek brown trout population, based on Akaike's information criterion (AIC_c)

Models and variables	AIC _c	ΔAIC _c	w _i
Models to explain variation in total population per capita rate of change			
dYOY (+)	42.15	0.00	0.72
dTotal (+)	44.97	2.82	0.18 (4.1 X)
Model to explain variation in adult population per capita rate of change			
dAdult (+)	87.55	0.00	0.91
Model to explain variation in yearling population per capita rate of change			
dYearling (+)	39.47	0.00	0.99
Models to explain variation in YOY population per capita rate of change			
dYOY (+)	62.42	0.00	0.45
dYearling (-)	63.73	1.31	0.23 (1.9 X)
dAdult (-)	63.91	1.49	0.21 (2.1 X)
dTotal (+)	65.27	2.85	0.11 (4.2 X)
Models to explain variation in YOY density			
Annual median Q (+)	25.48	0.00	0.31
May Q ₁₀ (-)	26.13	0.65	0.22 (1.4 X)
March mean Q (+)	27.60	2.12	0.11 (2.9 X)
March median Q (+)	28.02	2.54	0.09 (3.6 X)
May mean Q (-)	28.25	2.77	0.08 (4.0 X)
Annual mean Q (+)	28.90	3.42	0.06 (5.5 X)
May median Q (-)	29.74	4.36	0.03 (8.8 X)
March Q ₁₀ (+)	29.94	4.56	0.03 (9.8 X)
April Q ₁₀ (+)	29.95	4.57	0.03 (9.8 X)
Models to explain variation in cohort mortality rate			
dYOY (+)	-45.07	0.00	0.60
dTotal (+)	-44.21	0.86	0.40 (1.5 X)
Models to explain variation in PSS _Q			
Densities only			
dYOY _{t-2} (-)	164.41	0.00	0.48
dTotal _{t-2} (-)	165.15	0.74	0.33 (1.5 X)
dYOY _{t-1} (-)	167.94	3.53	0.08 (5.8 X)
dTotal _{t-1} (-)	168.66	4.25	0.06 (8.4 X)
Mortality rates only			
MortRate _{t-2} (-)	144.47	0.00	0.77
MortRate _t (-)	147.90	3.43	0.14 (5.6 X)
MortRate _{t-1} (-)	149.00	4.53	0.08 (9.6 X)
Models to explain variation in YOY fall weight			
dYOY (-)	103.04	0.00	0.63
dTotal (-)	104.34	1.30	0.33 (1.9 X)

Note. ΔAIC_c is the change in AIC_c between subsequent models, and w_i is the Akaike weight. Only models with w_i > 10% of the value of the best model are presented. Symbols in parentheses after variables indicate the direction of the correlation between response and explanatory variables. The comparative explanatory power of the best model (relative to each model) is shown in parentheses after w_i values. *d* is density (fish/m²), *Q* is discharge (m³/s), Q₁₀ is 10% exceedance discharge, and PSS_Q is proportional size structure-quality.

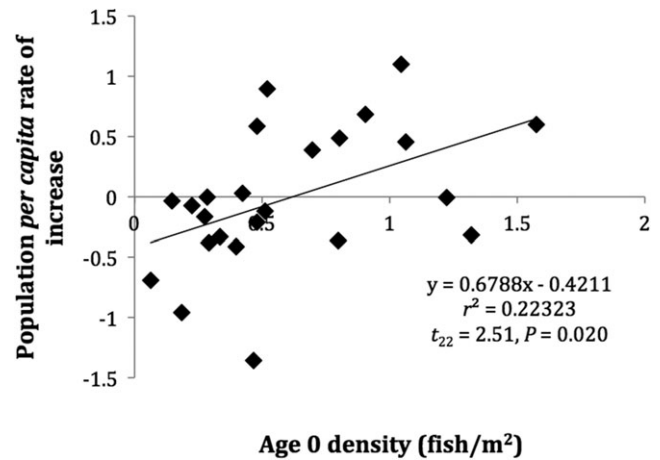


FIGURE 3 Relationship between fall densities of age 0 brown trout and per capita rate of increase of the total population in a 200-m stream site on Gilmore Creek, September–October 1989–2013 (model with greatest explanatory power from AIC analysis; see Table 2)

However, adult and yearling densities had strong effects on their respective per capita rates of change in subsequent years (Table 2). Densities of YOY fish had virtually no explanatory power (w_i = 0.0028; 354 times less likely) on per capita rate of change of yearling fish in subsequent years. In contrast, per capita rate of change of YOY trout was influenced to various degrees (both positive and negative) by densities of all age groups in the previous year (Table 2).

3.2 | Hydrology and recruitment

Nine simple models containing stream hydrology variables had varying degrees of explanatory power on fall densities of age 0 trout in Gilmore Creek (Table 2). High fall densities of age 0 fish occurred in years when annual discharges were above normal, March discharges were above normal, and May discharges were below normal. The two best models, annual median discharge and May Q₁₀ (10% exceedance discharge), held 53% of the total explanatory power (w_i) for all models combined. Annual median discharge correlated positively with age 0 trout density (Figure 4a), whereas high discharges during May (Q₁₀) correlated negatively with fall densities (Figure 4b). The highest discharges during May, the result of infrequent but heavy spring storm events, were correlated with low YOY densities (<0.6 fish/m²) during fall sampling. High fall densities of age 0 fish occurred only during years when May Q₁₀ discharges were low or moderate.

3.3 | Mortality rates

Mortality rates displayed large variations during the study period (range = 51–89%; Table 1). Additionally, mortality rates declined significantly over time (~20%; annual mortality rate = -0.0097 Year + 20.17, t(19) = 3.05, p = .007).

Mortality rates changed along with fish abundance, so AIC_c model selection was used to examine mortality rates versus total and age group densities. Models with age 0 or total densities best explained variation in mortality rates (Table 2, Figure 5).

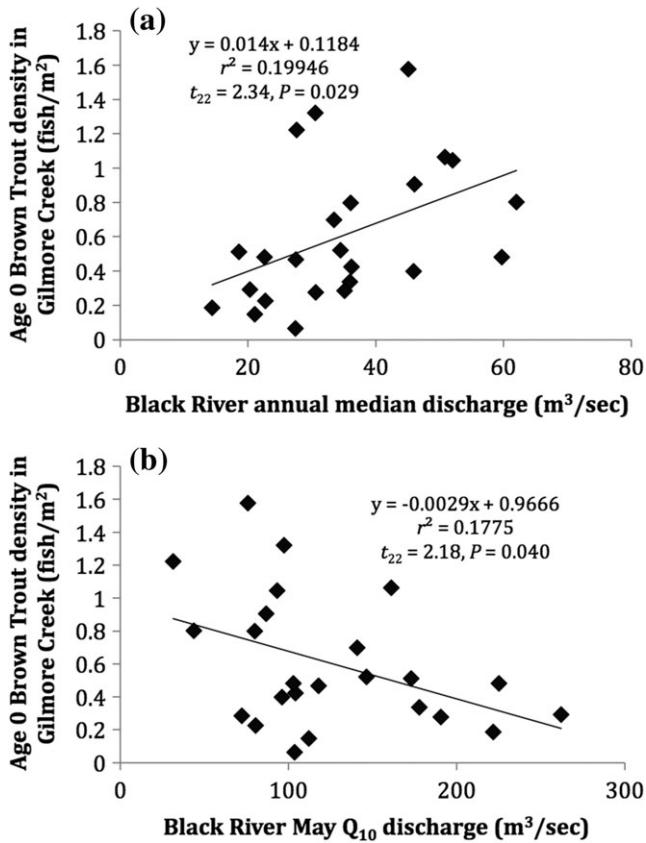


FIGURE 4 Relationships between fall densities of age 0 brown trout in a 200-m stream site on Gilmore Creek, September–October 1989–2013, and two measures of discharge for the nearby Black River: (a) median annual discharge vs. fish density; (b) May Q₁₀ (10% exceedance) discharge vs. fish density (models with greatest explanatory power from AIC analysis; see Table 2)

3.4 | Proportional size structure

The PSS indices highlighted the dominance of Gilmore Creek's brown trout population by young fish. Annual values for PSS_Q averaged 27% (Table 1), and PSS-preferred values were low (mean ± SD, 4 ± 5%; range = 0–23%), even though preferred-size fish (≥30 cm) were present during 20 of the 25 years. Extremely low PSS-memorable values (mean ± SD, 0.2 ± 0.5%; range = 0–2%) illustrate the scarcity (present during only 7 of 25 years) of memorable-size trout (≥38 cm).

The PSS_Q rose and fell repeatedly in a pattern opposite that of abundance (Table 1). Consequently, simple relationships (same year, 1-year, 2-year, and 3-year time lags) between PSS_Q and brown trout total and age group densities were explored using AIC_c model selection. Of the 16 models assessed, total and age 0 (YOY) densities with 2- and 1-year time lags had the most explanatory power for PSS_Q (Table 2). High densities of trout (age 0 and total) were associated with low PSS_Q 2 years later, and vice versa (Figure 6a,b).

Annual mortality rates also were correlated with changes in PSS_Q, with peaks in PSS_Q lagging 1 to 3 years behind lows in mortality rates. AIC_c model selection indicated that variation in PSS_Q was best explained by mortality rate with a 2-year time lag (i.e., by mortality rate of the cohort spawned 2 years earlier; Table 2, Figure 6c).

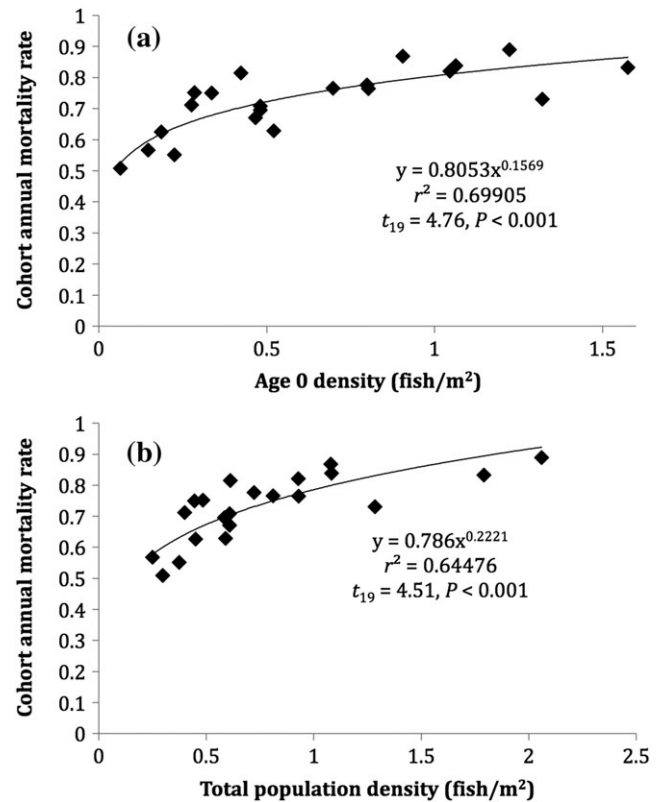


FIGURE 5 Relationships between brown trout cohort-based annual mortality rate and fall densities of age 0 (a) and total densities (b) in a 200-m stream site on Gilmore Creek, September–October 1989–2013 (models with greatest explanatory power from Akaike information criterion analysis; see Table 2)

Consequently, a high-density (>1 fish/m²) cohort with a high (>80%/year) cohort mortality rate led to reduced (<20%) PSS_Q (i.e., poorer size structure and probably reduced fishing quality) 2 years later.

3.5 | Density-dependent growth

Mean fall weights of age 0 trout averaged 9.2 g (SD = 2.3 g) but varied nearly threefold among years (range = 5.6–16.0 g). With the AIC_c model selection, variation in fall weights was best explained by densities of age 0 fish or by total density (i.e., density-dependent growth; Table 2, Figure 7a,b), but not with densities of fish age 1 and older (Figure 7c). Fall weights also were inversely correlated with annual mortality rates (simple linear regression: fall weight [g] = [−8.6802 * mortality rate] + 15.736, $r^2 = .175$, $t(21) = 2.11$, $p = .047$).

3.6 | Additional stream sites

Brown trout populations at the two additional, nearby stream sites cycled in general synchrony with the main study reach population (Figure 2), and YOY abundance and density were similar at all sites (Table 3). Neither annual mortality rates nor PSS_Q differed significantly among sites (Table 3), but both measures rose and fell at all sites in close synchrony. Mean fall weights of age 0 fish differed significantly among the three stream sites (Table 3), but fall weights were significantly and negatively related to age 0 densities at both Gilmore Creek-SMU (fall weight [g] = [15.057 * density (fish/m²)]^{−0.076},

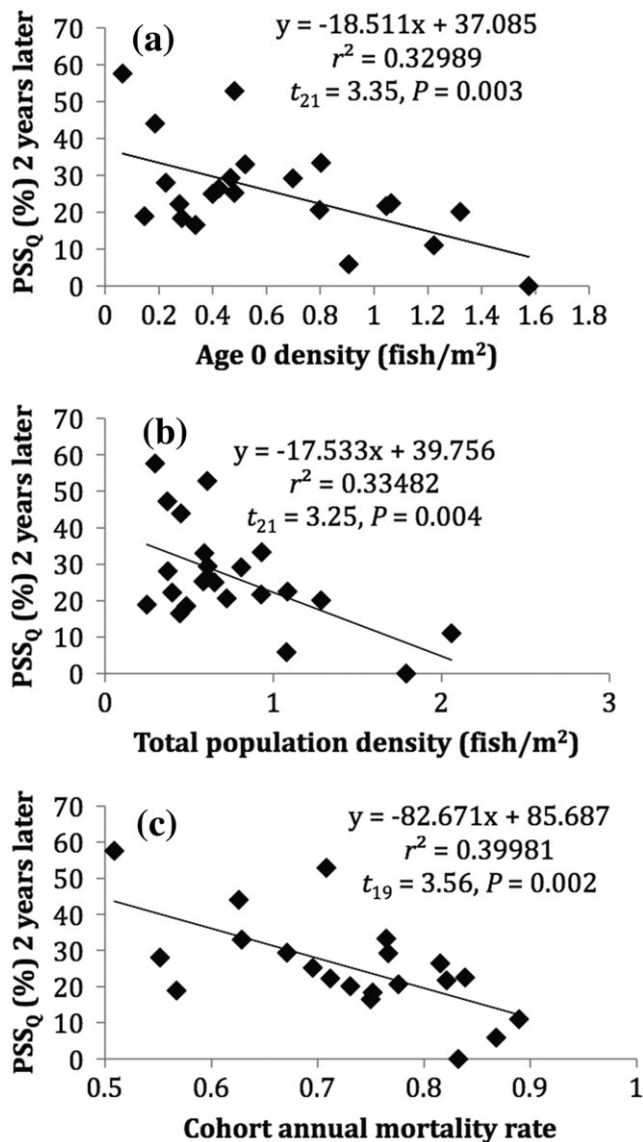


FIGURE 6 Relationships between PSS_Q (proportional size structure-quality) and fall densities of age 0 brown trout 1 year (a) and 2 years (b) earlier and cohort annual mortality rates 1 year earlier (c) in a 200-m stream site on Gilmore Creek, September–October 1989–2013 (models with greatest explanatory power from Akaike information criterion analysis; see Table 2)

$r^2 = .563$, $t(7) = 3.35$, $p = .012$) and Pleasant Valley Creek (fall weight [g] = $[15.859 * \text{density (fish/m}^2\text{)}]^{-0.238}$, $r^2 = .785$, $t(7) = 3.50$, $p = .013$) in a pattern similar to that at the main Gilmore Creek study reach (Figure 7a).

4 | DISCUSSION

This 25-year study revealed several key features of the brown trout population in a small, coldwater stream in southeastern Minnesota. First, the abundance of trout in Gilmore Creek fluctuated widely, due largely to changes in abundance of age 0 fish, with fish numbers within the study reach rising and falling in unison with trout numbers at other stream sites nearby. Second, the abundance of age 0 trout was correlated to regional stream hydrology, with high May discharges and

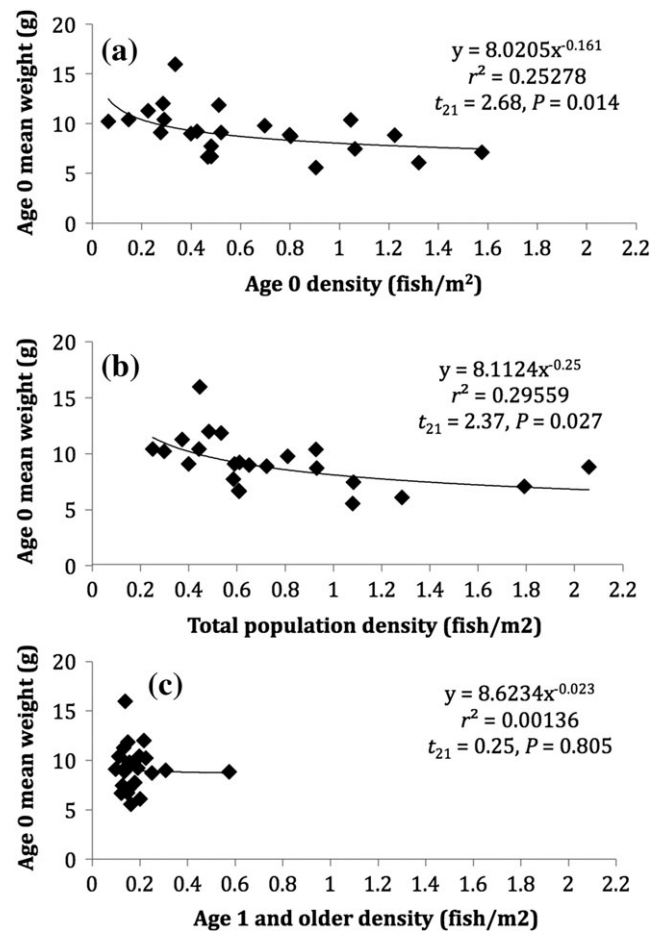


FIGURE 7 Relationships between mean weights of age 0 brown trout and (a) total population density, (b) age 0 fish density, and (c) density of age 1 and older fish in a 200-m stream site on Gilmore Creek, September–October 1989–2013 (models with greatest explanatory power from Akaike information criterion analysis; see Table 2)

annual baseline flows having opposing roles. Third, age 0 trout exhibited density-dependent growth and mortality rates. Finally, high-density cohorts of age 0 trout were inversely correlated with population size structure 2 years later. Taken together, these changing abundances and relationships can confound the interpretation of short-term studies (e.g., population response to habitat improvement, growth rate comparisons, size structure management, and creel surveys) of brown trout in similar systems.

Dramatic fluctuations in abundance of trout have been observed previously (e.g., Alonso et al., 2011; Lobón-Cerviá, 2007b; Zorn & Nuhfer, 2007a, 2007b). However, unlike those in Gilmore Creek, many of these fluctuations are truly cyclical when subjected to time series analyses. In Gilmore Creek, peaks in abundance resulted largely from periodic, strong year-classes and high recruitment (Lobón-Cerviá, 2011), with peaks occurring simultaneously within three separate stream reaches during the final 11 years of the study.

Salmonid populations can fluctuate in synchrony regionally (e.g., Cattaneo et al., 2003; Lobón-Cerviá, 2007b; Zorn & Nuhfer, 2007b). Geographic synchronization of abundance is not unique to trout, or even to fish in general (Bjørnstad, Ims, & Lambin, 1999). Proposed mechanisms underlying regional synchronization (i.e., Moran

TABLE 3 Population variables for brown trout at three streams sites in Winona, Minnesota, 2003 to 2013

Variable	Gilmore Creek-Wildwood	Gilmore Creek-SMU	Pleasant Valley Creek	<i>p</i>
Age 0 population estimate	353 (245)	196 (231)	186 (110)	.144
Age 0 density (fish/m ²)	0.36 (0.21)	0.23 (0.25)	0.21 (0.12)	.217
Annual mortality rate (%)	0.67 (0.11)	0.67 (0.17)	0.74 (0.09)	.392
Age 0 mean weight (g)	9.68 (1.48)	17.87 (2.37)	25.07 (5.05)	<.001
Proportional size structure (%)	33.3 (12.8)	44.3 (23.0)	41.1 (23.0)	.451

Note. Values are means with standard deviations in parentheses. *p* values are for the "site" variable only from two-factor ANOVAs (site X year).

effect) include dispersal, climate patterns, hydrology, and trophic level interactions (Liebhold, Koenig, & Bjørnstad, 2004). Synchrony among brown trout population abundances has been linked to high flow rates (i.e., spring flooding) during the critical spring emergence period that reduce densities of age 0 trout (Alonso et al., 2011; Cattaneo, Lamouroux, Breil, & Capra, 2002; Cattaneo et al., 2003; Zorn & Nuhfer, 2007a, 2007b).

In Gilmore Creek, fall densities of age 0 trout were inversely correlated with May Q_{10} discharge magnitude in a nearby gaged stream. Conversely, high annual baseline (median) flows were positively correlated with fall densities of age 0 trout. Together, these hydrologic variables accounted for >30% of the variability in fall densities of age 0 trout in Gilmore Creek. Fall densities did not exhibit any significant parabolic or two-phase regression relationship with discharge during any spring month (Lobón-Cerviá, 2007b; Lobón-Cerviá & Rincón, 2004) that would indicate higher survival of young fish during years with intermediate discharges. When high-intensity storm events produced high discharges in May, newly emerged trout fingerlings suffered high mortality, leading to low densities of age 0 fish during fall (Cattaneo et al., 2003; Zorn & Nuhfer, 2007a). When high discharges were lacking in May, mortality among brown trout fingerlings was reduced, resulting in higher fall densities for age 0 trout, especially under high baseline flows.

Peaks in fall abundance of age 0 trout in Gilmore Creek generally occurred during years when La Niña influenced weather patterns in southeastern Minnesota (U.S. National Weather Service, Climate Prediction Center website: http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml). La Niña produces colder winters with above average snowfall in Minnesota, resulting in greater recharge of aquifers (Delin, Healy, Lorenz, & Nimmo, 2007) and higher stream base flows throughout summer and fall in groundwater-based streams in southeastern Minnesota (Waters, 1977). Peaks in annual median discharge in the Black River coincided with peaks in densities of age 0 trout in Gilmore Creek, suggesting a potential link between La Niña and regional abundances of stream-dwelling brown trout.

One additional hydrologic factor affected fall densities of age 0 trout in Gilmore Creek. Extreme flood events occurred irregularly during summer months throughout the study, differing in magnitude and duration. One such event occurred over a 48-hr period during August 2007 (one-in-2000-year flood magnitude; Keillor, 2010). This single event eliminated the majority of age 0 trout in Gilmore Creek (see Figure 1) and in many regional streams.

During years when YOY trout abundance was high in Gilmore Creek, growth rates were reduced and mortality rates increased. Density-dependent growth of juvenile brown trout has been reported at locations in North America and Europe (e.g., Lobón-Cerviá, 2007a,

2007b; Richard, Cattaneo, & Rubin, 2014; Sundström, Kaspersson, Näslund, & Johnsson, 2013; Zorn & Nuhfer, 2007a), with growth rates consistently slowest when densities are >1 YOY/m² (Jenkins et al., 1999; Lobón-Cerviá, 2007a). Mass-based growth rates of YOY trout decrease approximately 15% as fish density doubles (Grant & Imre, 2005; Jenkins et al., 1999); fish in Gilmore Creek displayed a 38% decrease in mean fall mass as YOY densities increased from 0.1 to 2.0 YOY/m². Such reductions in growth have been attributed to intra-specific competition, specifically exploitation and interference competition (Grant & Imre, 2005).

Mortality rates of brown trout display wide variability among rivers, seasons, years, and cohorts (Carlson & Letcher, 2003; Cunjak & Power, 1987). Gilmore Creek mortality rates averaged >70%, similar to values reported for brown trout in other systems (Carlson & Letcher, 2003). In addition, mortality rates of successive cohorts of trout in Gilmore Creek frequently differed by >20%, with mortality rates often declining dramatically in years following very high rates. Fluctuations in trout mortality rates can result from both changing food availability (brought on by competitive interactions) and varying climatic conditions (Carlson & Letcher, 2003; Cunjak & Power, 1987).

Mortality rates in Gilmore Creek were strongly, positively correlated to densities of YOY trout, with mortality exceeding 80% when YOY densities were >1 fish/m². Higher mortality rates associated with higher density cohorts can affect a cohort throughout its time in the system, not just during YOY or yearling stages (Lobón-Cerviá, 2005, 2007b). High trout densities tend to reduce growth rates before increasing mortality, thereby acting to maintain higher population abundance (Lobón-Cerviá, 2005, 2007a; Lobón-Cerviá & Mortensen, 2005). Consequently, intense competition for food and space within higher density cohorts continues to stress individuals throughout their entire lives (Carlson & Letcher, 2003; Dieterman & Hoxmeier, 2011), resulting in higher mortality rates for the duration of the cohort. When trout densities were high in Gilmore Creek, age 0 fish grew slowly and were small (8 g) during their first fall. Small fish experienced high mortality rates (80–90%) during the following year and subsequently continued to exhibit annual mortality rates at least 10% higher than those observed in low-density cohorts.

High, density-dependent mortality rates observed for brown trout between ages 0 and 1 in Gilmore Creek are in partial conflict with recent reports (Lobón-Cerviá, 2012; Lobón-Cerviá et al., 2012) from Europe. Brown trout in Gilmore Creek experienced mortality rates averaging >70% between their first and second September of life (ages of 6 and 18 months), but trout in several streams in Denmark and Spain exhibited negligible mortality during the same life stage, with most mortality occurring only in adult fish. Although Gilmore Creek trout

demonstrated a three-phase pattern of mortality (early phase with severe mortality, second phase with weaker mortality, and third phase with severe mortality) generally resembling that reported for brown trout in a single stream in Denmark (Lobón-Cervia et al., 2012), the first phase apparently lasted >3× longer in Gilmore Creek (18 vs. 5 months). The reason for these differences in patterns of mortality is unknown, although it may be related to differences in age structure between Gilmore Creek (spawning fish ages 2 or 3, or older) and the European populations (spawning fish ages 1 and 2).

With varying trout densities and mortality rates, PSS_Q also fluctuated widely. The highest PSS_Q values (>40%) in Gilmore Creek occurred 1 or 2 years after appearance of low-density cohorts, whereas low PSS_Q values (<20%) occurred 1 or 2 years following high-density cohorts. Similar correlations between reduced adult abundances and increased fish densities, including multiyear time lags, have been reported in other fish species (Phelps, Ward, Paukert, Cripps, & Willis, 2005; Pierce, Tomcko, & Margenau, 2003; Rose, Cowan, Winemiller, Myers, & Hilborn, 2001). In Gilmore Creek, these correlations suggest that the best trout size structure occurred 2 years after a weak year-class of age 0 fish experienced reduced mortality and subsequently increased recruitment to the adult population. This concept is in opposition to typical fisheries management theory, where a strong year-class subsequently leads to improved numbers of adult fish in future years. Within the Gilmore Creek population, high YOY abundance during fall was a harbinger of increased mortality, reduced adult abundance, and poorer fishing.

4.1 | Management implications

Density-dependent growth and mortality rates and fluctuating population dynamics displayed by brown trout in Gilmore Creek likely are not unique among the streams within the Driftless Area. This region spans >60,000 km² and contains >600 limestone spring-fed creeks (Hastings & Hewitt, 2008), with these high-alkalinity streams among the most productive salmonid streams in the United States (Kwak & Waters, 1997). Although these streams vary in water temperature, prey availability, and trout growth rates (Dieterman et al., 2004; Troelstrup & Perry, 1989), they increasingly are being protected, restored, and managed as a unit (Hastings & Hewitt, 2008), with variations in angling regulations to achieve both social and scientific goals (Minnesota DNR, 2011).

Density dependence in growth rates, mortality rates, and population size structure of brown trout populations likely can complicate or confound interpretations of short-term studies of this species within streams of the Driftless Area. The present study clearly demonstrates that 1- or 2-year “snapshots” of data from Gilmore Creek produce widely differing conclusions. For example, a 2-year study in 1997 and 1998 would conclude that trout in Gilmore Creek exist at high densities (nearly 2 fish/m²), experience mortality rates >80%, and exhibit poor size structure for fishing ($PSS_Q < 20\%$). In contrast, a 2-year study in 2007 and 2008 would find low densities (0.3 fish/m²), low annual mortalities (<60%), and better size structure ($PSS_Q = 25\text{--}50\%$). Management plans developed for this stream on the basis of either of these two, time-period studies alone would be inappropriate.

Unfortunately, interpretation of short-duration (1 to 3 years) studies of brown trout in streams of the Driftless Area has been the basis for many past and current management decisions. Studies of brown trout growth rates (Dieterman et al., 2012), creel surveys (Snook & Dieterman, 2014), habitat improvement evaluations (Hunt, 1988), and regulation evaluations (Thorn, 1990) become complicated when abundances of fish fluctuate dramatically and when growth and mortality rates are density dependent. Studies investigating population responses to improved habitat or modified angling regulations need to cover a period spanning several generations of brown trout, to account for the background “noise” associated with natural fluctuations in mortality and abundance (Zorn & Nuhfer, 2007a, 2007b). Efforts to improve growth rates (Dieterman et al., 2004) and to increase the abundance of large trout for anglers (Minnesota DNR, 2000) might need reevaluation, as significant improvements in growth rate and higher, sustained PSS_Q likely will occur only in systems where brown trout populations can be maintained at densities where competition for food is not limiting (*sensu* Pierce et al., 2003).

Clearly, long-term monitoring efforts (Minnesota DNR, 2011) are needed to better understand the dynamics of brown trout populations within streams of the Driftless Area, especially in light of possible climate change effects on these fisheries (Jensen et al., 2008). Because stream salmonid fisheries provide a \$1.1 billion annual economic impact to this region and millions of dollars have been and continue to be spent to protect and restore them (Hart, 2008), a comprehensive understanding of the biology of brown trout in these streams is imperative.

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