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Growth and Production of Juvenile Trout in Michigan Streams: Influence of Temperature

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Abstract.–Thermal conditions and trout population characteristics were followed at 17 sites in northern lower Michigan over a 3-year period to determine the influence of temperature on growth and production of juvenile brook trout *Salvelinus fortinalis* and brown trout *Salmo trutta*. Thermal regimes were summarized from 25 separate indicators using principal components analysis. The first two principal axes accounted for 99.8% of the variation in the summarized temperature variables. The first component was strongly and negatively correlated with summer mean temperature (r=-0.98) while the second principal component was most strongly correlated with mean winter temperature (r=0.95). Growth rate of juvenile brook trout was not significantly correlated with density of juvenile brook or brown trout. Growth rate of juvenile brown trout was not significantly correlated with density of juvenile brook trout, but was negatively correlated with density (r=-0.52) and standing stock (r=-0.46) of juvenile brown trout. Temperature principal components explained 29.7% of the variation in the growth rate of juvenile brook trout and 47.6% of the variation in the growth rate of juvenile brown trout. Addition of density of juvenile trout to these models improved the fit to 33.5% for juvenile brook trout growth rate but did not improve the fit of the growth rate model for juvenile brown trout (R^2=0.45). Production, as measured by standing stocks of juvenile brook and brown trout, was not significantly correlated with either principal temperature component. In order to allow for greater use of the data collected for this study, the basic temperature summaries were used to form simple linear regression (SLR) models for growth rate and standing stock of juvenile brook and brown trout. The best simple model for growth rate of juvenile brook trout explained 48.2% of the variance from the mean daily temperature fluctuation in July. The best brown trout growth rate model explained 53.1% of the variance using the mean daily temperature for the month of July. These types of data are easily collected by fisheries managers and will allow for estimation of expected growth rates at sites containing juvenile brook or brown trout.

While lethal thermal limits for trout in laboratory settings have long been established (e.g., Fry et al. 1946) the influences of temperature on trout living within their range of thermal tolerance is poorly understood. Temperature can be considered a master variable with respect to growth and production of fish due to its influence on both rates of metabolism and foraging activity. Brett (1979) lists temperature, ration, and size of fish as the three main factors influencing the growth of fish. Elliott (1994) has examined thermal influences on growth and production of brown trout *Salmo trutta* in a series of laboratory and field studies. By following characteristics of fish populations (e.g., growth rate, density, standing stock) and temperature in a variety of streams differential responses to the thermal regime can be observed. Growth rates of trout have been shown to vary in association with major seasonal temperature changes (Cooper 1953; McFadden 1961; Hunt 1966). Generally, increased growth occurs at higher temperatures (e.g., Johnson et al. 1992) and lowered growth occurs at colder temperatures (Cunjak and Power 1987; Cunjak et al. 1987). High summer temperatures cause slowed growth when energy intake falls below that required for maintenance metabolism (Ensign et al. 1990).

The major objective of this study was to determine the relationships between temperature, growth and production of juvenile trout in streams in the northern Lower Peninsula of Michigan. We estimated growth rate and production of juvenile brook trout *Salvelinus fontinalis* and juvenile brown trout from 12 small streams in the northern Lower Peninsula of Michigan and five large sites on the Au Sable River. These data were used to examine the proportion of the variance in growth rate and productivity of juvenile trout explained by thermal conditions at these sites.

Methods

The 12 small stream sites were selected to represent small stable trout streams (Horton-Strahler stream order of <4) based on a survey of over 500 sites throughout the lower peninsula of Michigan (Kohler and Wiley 1991). An additional five larger survey sites from the Au Sable River (two on each of the North Branch and Main stem and one on South Branch) were selected to coincide with previous and concurrent data collections by the Fisheries Division of the Michigan Department of Natural Resources. Location of sample sites is shown in Figure 1.

Temperature (°C) was monitored at each site with minimum-maximum thermometers (1993, read monthly) and electronic thermographs (Au Sable sites 1993, all sites 1994-95) set at measurement intervals of 60 or 96 minutes. Measurements collected at each site with the thermographic recorders were summarized into daily and monthly mean, maximum, and minimum termperatures, and accrual of thermal units (ATUs, i.e., degree days). Mean daily temperature fluctuation (Flux) was the difference between daily maximum and minimum temperatures. Missing data were estimated from predictive equations developed from between site water temperature records. Data were further summarized using these daily summaries into annual, winter (November-April), summer (May-October), February, and July time periods.

Fish sampling at small stream sites was conducted in late fall of each year (usually December) at each site when possible (ice cover precluded sampling in some years). Fall sampling included a 3-pass removal estimate (Zippen 1958) or a mark-recapture estimate using the Bailey modification (Bailey 1951; Cooper and Ryckman 1981) made with electroshocking gear. The size of the reach sampled was set by the size of the stream and was not less than 100 feet in length at the smallest site. Fish sampling at the five larger Au Sable River sites included mark-recapture estimates made in late summer of each year. Total length (mm) and/or mass (grams) of all fish collected were measured for individual fish. A series of scale samples was also collected from trout at all sites to identify age 0 fish.

Trout were conservatively defined as juveniles for this study if their total length was ≤100 mm (3.94 inches) and they were age 0. Immature status was assumed based on a fall study at one of our study streams, Hunt Creek, by McFadden et al. (1967). They found no mature brook trout <5 inches long and no age 1 trout <4 inches long.

Growth rates (g wet mass/day) were estimated for each sampling date from size of juvenile trout assuming all fish were born on January 1 of that year. Standing stock of juvenile trout was used as a surrogate for production in this study since multiple measurements of fish size were not made within the same year and all fish were age 0.

Statistical analyses were performed using Data Desk (Velleman and Capehart 1995). Where necessary, variables were normalized by square root transformations. Techniques used were simple correlation, principal component analysis (PCA), multiple linear regression (MLR) and simple linear regression (SLR).

Results

Thermal characteristics

Mean annual ATUs were generally highest at the large sites, particularly for the Au Sable River (Table 1). Small sites had lower maximum temperatures and higher minimum temperatures. Only three sites had annual maximum temperatures below 20°C. Two of these, plus Hunt Creek, were the only sites with minimum temperatures above 0°C. The South Branch of Spring Brook, for example, had the lowest maximum temperature (14.0°C) and the highest minimum temperature (2°C). Winter mean daily temperatures ranged from 1.3°C at Antrim Creek to 5.9°C at Roaring Brook. Summer mean temperatures were generally below 14°C for non-Au Sable River sites with the exception of Antrim Creek (14.4°C). July temperatures followed a pattern similar to the summer period but were higher with mean daily temperatures from 9.5°C at SB Spring Brook to 18.4°C at Chase Bridge and Dam Four.

Mean daily water temperature at the study sites over the entire sampling period (1993-95) varied between 6.2§C and 10.7§C (Table 2). The highest and lowest maximum annual temperatures recorded were 27.4§C and 11.9§C. Annual minimum temperatures varied between -2.4§C and 3.0§C. Total accumulated thermal units (ATUs) varied between 2276 and 4029 for all sites and years.

Seasonal daily mean water temperatures for all sites averaged 3.6§C during the period from November 1 through April 30 (winter) and 12.4§C during the period from May 1 through October 30 (summer) (Table 3). Average maximum temperatures were 11.3§C during winter and 20.9§C during the summer. Average minimum temperatures were -0.1§C during winter and 4.6§C during summer. Winter ATUs ranged from 152 to 1672 while summer ATUs varied between 1506 and 2955 for all sites during the course of the study. Mean daily water temperatures for two months that were selected as extremes for the winter (February) and summer (July) periods were 2.1§C and 15.1§C, respectively. Average February and July ATUs were 59 and 469.

Annual mean temperature was positively and highly correlated (r=0.67) with annual maximum temperature (Table 4). In general, annual maximum temperatures were positively correlated with summer temperature summaries and negatively correlated with winter temperature summaries while annual minimum temperatures had the opposite trend. February and July temperature summaries were highly correlated with, and behaved similar to, winter and summer temperature summaries, respectively.

Principal components analysis revealed that the first two principal axes accounted for 99.8% of the variation in temperature summary variables (Table 5). The first principal component was most strongly (negatively) correlated with summer temperature summaries such as summer mean (r=-0.98) and summer ATUs (r=-0.98) (Table 6). The second principal component was most strongly (positively) correlated with winter temperature summaries such as mean temperature (r=0.95) and February maximum temperature (r=0.80).

Trout populations and growth

Mean density of juvenile brook trout was lowest at Big Creek (11/ha or 0.06 kg/ha) and highest in the headwaters of the Rapid River (5776/ha) in terms of numbers of trout, and at Hunt Creek (27.7 kg/ha) for standing stock biomass (Table 7). Juvenile brown trout were not present in collections at seven sites at any time during the study (Table 8). Mean brown trout density among sites where they were collected was lowest at Hunt Creek (10/ha or 0.05 kg/ha) and highest at Belanger Creek (3307/ha or 18.91 kg/ha).

Average juvenile brook trout growth was 0.0170 g wet wt./day for all 17 sites during the study period (Table 9). Juvenile brook trout density ranged from 0 to 6960 trout per hectare (0 - 38.1 kg/ha). For the eight sites without juvenile brown trout present, average growth was a bit lower at 0.0125 g wet wt./day and densities of juvenile brook trout ranged from 89 to 6960 trout per hectare (0.3 - 38.1 kg/ha).

Average juvenile brown trout growth was 0.0230 g wet wt./day and densities ranged from 31 to 4997 trout per hectare (0.16 - 27.5 kg/ha) for the 10 sites where juvenile brown trout were collected during the study period (Table 10). Juvenile brown trout density ranged from 0 to 4997 trout per hectare (0 - 27.5 kg/ha) across all 40 site-date combinations.

Growth of juvenile brook trout was not significantly correlated with densities of juvenile brook or brown trout (Table 11). Juvenile brown trout growth was not correlated with juvenile brook trout density, but was negatively correlated with both numbers (r=-0.52) and standing stock (r=-0.46) of juvenile brown trout. Growth rates of juvenile brook and brown trout were highly correlated (r=0.88).

Temperature and growth

Growth of juvenile brook trout was positively correlated with most annual and summer temperature summary statistics but not with winter temperature summaries, with the exception of winter maximum temperature (r=0.42) (Table 12). Juvenile brown trout growth was found to be most highly correlated with July (r=0.73) and summer (r=0.72) mean temperatures and with annual maximum temperature (r=0.66).

The first two principal components of the temperature summary variables explained nearly 30% of the variance in growth of juvenile brook trout when all sites were combined (Table 13). There was no significant relationship between the two principal components and growth of juvenile brook trout when only sites with no juvenile brown trout were examined. Nearly half (48%) of the variation in juvenile brown trout growth was explained by the temperature summary principal components.

Temperature principal components and juvenile trout density explained 34% of the variation in the growth rate of juvenile brook trout (Table 14). The same model did not explain a significant portion of the variation in the growth of juvenile brook trout when only sites that did not contain juvenile brown trout were considered. Temperature principal components and juvenile trout density explained over 45% of the variation in juvenile brown trout growth rate.

Similar relationships could be seen using simple temperature parameters in place of the principal components (Table 15). For example, summer mean and winter mean temperatures explained 29% of the variation in growth of juvenile brook trout. A similar model was not a significant predictor for sites that did not have juvenile brown trout present. Summer mean and winter mean temperatures explained 34% of the variation in growth of juvenile brown trout. Summer and winter mean temperatures when combined with juvenile trout density explained 43% of the variation in juvenile brown trout growth rate.

Temperature and density

Juvenile brook trout density (number/ha) was negatively correlated with July mean temperature (r=-0.42) and positively correlated with daily winter temperature fluctuation (r=0.33, Table 12). Standing stock (kg/ha) was positively correlated with daily annual temperature fluctuation (r=0.38). Numerical density of juvenile brook trout was positively correlated with the first principal component (r=0.41) while standing stock was not significantly correlated with either principal component (Table 6). There was a weak positive relationship between the density (number/ha) of juvenile brook trout and the two principal components (R^2=0.13) in a combined model (Table 13).

No significant correlations were found between juvenile brown trout densities (number/ha) and any of the temperature summaries. Brown trout standing stock was found to be negatively correlated with summer minimum temperatures (r=-0.36) and positively correlated with winter maximum temperatures (r=0.34, Table 12). Neither juvenile brown trout density nor standing stock were significantly correlated to either principal component (Table 6). There was no significant relationship with density of juvenile brown trout in a combined model including the first two principal components and a very weak (R^2=0.13) relationship with standing stock (Table 13).

Simple single-parameter models

Many of the temperature summary statistics used in the above analyses require long term temperature records covering complete years. While these data describe the overall thermal regime that is experienced by trout at these sites, these types of data are frequently difficult to obtain. In order to allow for greater use of the data collected for this study the basic temperature summary statistics were used to form simple linear regression (SLR) models for growth and standing stock of juvenile brook and brown trout (Table 16). The best simple model for growth of juvenile brook trout explained 48% of the variance from the mean daily temperature fluctuation in July. The best brown trout growth model explained 53% of the variance using the mean daily temperature for the month of July. Production of juvenile brook and brown trout was not well explained by SLR models of this type and are not reported in this study. The maximum variation in production (standing stock) of juvenile brook or juvenile brown trout in this study was less than 23%, and most SLR models explained less than 10% of the variance.

Discussion

Temperature variables seemed to influence the two species in similar ways at the first level of analysis (e.g., annual maximum temperature was highly correlated to both species growth rates). However, MLRs with the PCAs suggest that these species respond to their thermal environment differently. The relationship between growth and PCA2 is positive for brook trout and negative for brown trout (Table 13). Similarly, although not statistically significant, the signs of the coefficients between standing stocks of brook and brown trout juveniles differed for PCA1 and PCA2 (Table 13). Differences in the response of brook and brown trout to their thermal regime have been noted elsewhere. Latta (1965) found a highly significant linear correlation between numbers of young-of-the-year brook trout and ground water levels that he associated with moderated temperatures. He found no correlation between ground water levels and numbers of young-of-the-year brown trout in the same locations. The current study suggests that growth was related to temperature but a large fraction of the variation remains unexplained. Growth rates of the two trout species were highly correlated (r^2=0.88, Table 11) where they co-occurred suggesting that some of the sites were better for the growth of trout regardless of species. This may have been due to temperature, food availability, or some combination of those and other factors.

Density dependence in trout populations

Evidence of density-dependent growth in trout populations has been widely reported. Fingerling trout growth was negatively correlated to their density in a study of three populations of wild brook trout (Carline 1977). Negative correlations between size (mean length and mean weight) and brook trout population density in Wyoming beaver ponds suggests that growth decreased as density increased (Johnson et al. 1992). These studies would suggest that density dependence is routinely important to the growth of juvenile trout in running waters. However, growth of age 0 brook trout was found to vary little during the 14-year study reported by McFadden et al. (1967) while their densities varied nearly 2.4 times. Density dependence did not appear to be a significant factor effecting brook trout rates in our study. However, we found juvenile brown trout growth rates were significantly correlated to their own density (r=-0.52) and standing stock (r=-0.46, Table 11).

The mechanisms leading to density dependent responses may be complex. Several studies suggest that growth rates are relatively fixed for a given species at a given site, implying either compensatory growth or rapid numerical responses to density related stresses. For example, instantaneous growth rates of brook trout did not vary significantly within or among populations despite large differences in population densities in spring-fed ponds of northern Wisconsin (Carline 1977). One potential mechanism for this is McFadden and Cooper's (1964) suggestion that in some populations of brown trout numerical adjustments to density and food supply precede growth rate adjustments and effectively reduce growth rate variation. A similar adjustment appears to have occurred among brook trout in the bed load manipulation experiments in Hunt Creek where experimentally induced reductions in food supply led to large declines in density but minimal changes in growth (Alexander and Hansen 1988).

Nicieza and Metcalfe (1997) suggest that growth rate is normally submaximal and can be improved by increasing consumption in juvenile Atlantic salmon *Salmo salar*. They found that compensatory growth occurred after low temperature or decreased ration induced growth depression. This suggests that if prey availability allows for increased rations, salmonids can increase their growth rates by increasing consumption and that over long time frames short term deficits can be averaged out. Prey availability is essential in this regard since compensatory growth can only occur when energy intakes are in excess of daily requirements.

Food organism abundance has been found to be positively correlated with the growth rate of brook trout (Cooper 1953). However, variability of food organisms in trout streams is notoriously high (Leonard 1939; Needham and Usinger 1956). Many streams included in our study have experienced wide fluctuations in macroinvertebrate abundance associated with complex dynamics involving parasites of dominant caddisfly populations (Kohler and Wiley 1997). If potentially available ration differs dramatically from year to year, then it is not unexpected to have difficulty in detecting thermally induced variation in trout growth. Additional research evaluating the linkages between available ration and thermal characteristics may improve our understanding of the mechanisms underlying the growth of juvenile trout.

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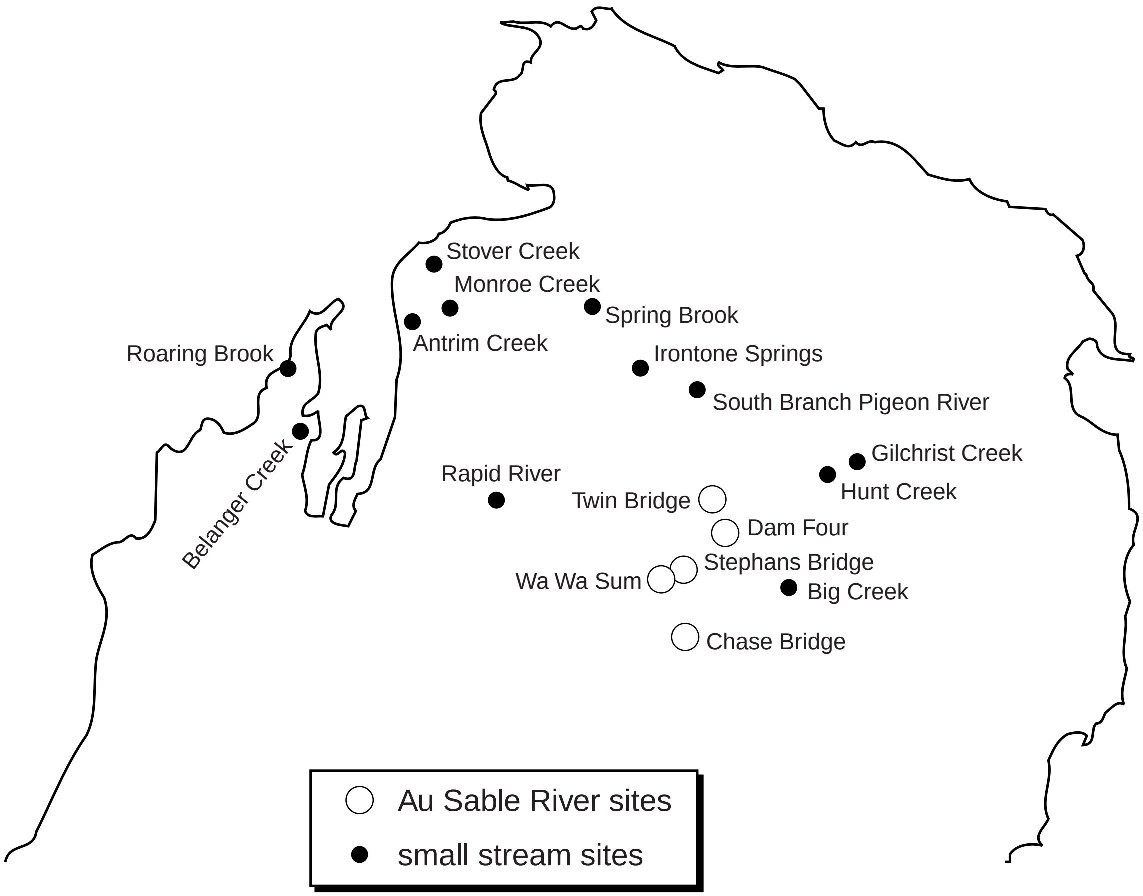

SITE	T. R. S.		
Antrim Creek	T. 32 N.	R. 9 W.	S 14
Belanger Creek	T. 30 N.	R.11 W.	S 10
Big Creek	T. 26 N.	R. 1 E.	S 24
Chase Bridge	T. 25 N.	R. 2 W.	S 22
Dam Four	T. 27 N.	R. 1 W.	S 4
Gilchrist Creek	T. 29 N.	R. 3 E.	S 27
Hunt Creek	T. 29 N.	R. 2 E.	S 35
Irontone Springs	T. 31 N.	R. 3 W.	S 15
Monroe Creek	T. 33 N.	R. 7 W.	S 31
Rapid River	T. 28 N.	R. 6 W.	S 18
Roaring Brook	T. 31 N.	R.11 W.	S 7
Pigeon River	T. 31 N.	R. 2 W.	S 35
Spring Brook	T. 33 N.	R. 4 W.	S 33
Stephans Bridge	T. 26 N.	R. 2 W.	S 5
Stover Creek	T. 34 N.	R. 8 W.	S 35
Twin Bridges	T. 28 N.	R. 2 W.	S 13
Wa Wa Sum	T. 26 N.	R. 2 W.	S 7

Figure 1.—Locations of study sites in northern Lower Michigan.

Table 1.–Selected temperature summaries for 17 sites sampled in 1993-95. Winter period is from November 1 through April 30; summer period is from May 1 through October 30. Temperature was measured in °C. (Au) = Au Sable River site. ATU = accumulated thermal units.

	Annual			Seasonal		July		
	Mean	Period of record		Winter	Summer	Daily	Daily	N
Site	ATU	Maximum	Minimum	mean	mean	mean	flux	(years)
Antrim Creek	2872	21.4	-2.4	1.3	14.4	16.5	2.3	3
Belanger Creek	2889	22.0	-2.0	3.7	12.1	15.8	2.2	3
Big Creek	2999	24.0	-0.8	4.1	12.3	15.7	4.3	3
Chase Bridge (Au)	3306	25.4	-0.4	2.8	15.2	18.4	3.7	2
Dam Four (Au)	3213	26.7	-0.4	2.9	14.6	18.4	6.4	1
Gilchrist Creek	3182	22.6	-1.0	4.6	12.8	16.6	3.9	3
Hunt Creek	2797	20.3	0.3	3.8	11.4	13.9	4.5	3
Irontone Springs	2489	21.0	-0.3	2.5	11.1	13.0	2.1	3
Monroe Creek	3283	24.0	-0.8	4.4	13.5	16.6	2.8	3
Rapid River	2527	17.0	-1.1	3.6	10.2	12.0	3.3	3
Roaring Brook	2901	17.0	1.4	5.9	10.0	11.2	1.2	3
SB Pigeon River	2760	22.0	-1.8	2.9	12.9	16.7	3.5	3
SB Spring Brook	2652	14.0	2.0	5.8	8.7	9.5	1.2	3
Stephans Bridge (Au)	3213	25.4	-0.4	3.4	14.1	17.3	3.7	2
Stover Creek	2753	22.1	-0.5	2.0	13.0	15.8	2.8	2
Twin Bridges (Au)	3322	27.4	-0.4	3.2	14.9	18.1	5.4	1
Wa Wa Sum (Au)	3197	24.2	-0.3	3.2	14.2	17.9	3.4	3

Table 2.–Annual temperature summaries for 17 sites sampled in 1993-95. Only complete annual records were used. Temperature was measured in °C.

Statistics	Daily mean	Annual maximum	Annual minimum	Daily flux	Accumulated thermal units
N	44	44	44	44	44
Mean	8.01	20.77	-0.09	2.42	2925
Stnd. Dev.	0.88	3.56	1.07	0.63	328
Median	7.95	21.50	-0.20	2.40	2897
Maximum	10.70	27.40	3.00	4.10	4029
Minimum	6.20	11.90	-2.40	1.20	2276
Range	4.50	15.50	5.40	2.90	1753

Table 3.–Seasonal and representative monthly temperature summaries for pooled sites and dates. Values were derived from individual site statistics. Winter period is from November 1 through April 30; summer period is from May 1 through October 30. Temperature was measured in °C.

Statistics	Daily mean	Maximum	Minimum	Daily flux	Accumulated thermal units
Winter					
N	44	44	44	44	44
Mean	3.63	11.33	-0.08	1.99	657
Stnd. Dev.	1.66	3.27	1.10	0.62	302
Median	3.30	11.10	-0.20	1.95	597
Maximum	9.20	25.40	3.30	3.70	1672
Minimum	0.80	6.10	-2.40	1.10	152
Range	8.40	19.30	5.70	2.60	1520
Summer					
N	44	44	44	44	44
Mean	12.39	20.89	4.64	2.85	2277
Stnd. Dev.	1.90	3.67	1.54	0.97	352
Median	12.65	21.65	4.90	2.85	2329
Maximum	16.10	27.40	6.70	5.50	2955
Minimum	8.20	11.90	-2.00	1.20	1506
Range	7.90	15.50	8.70	4.30	1449
February					
N	44	44	44	44	44
Mean	2.11	4.78	0.20	2.21	59
Stnd. Dev.	1.89	2.54	1.17	1.48	53
Median	1.80	4.50	0.00	1.60	50
Maximum	9.30	16.80	3.30	6.50	259
Minimum	-1.00	1.00	-2.30	0.40	-28
Range	10.30	15.80	5.60	6.10	287
July					
N	44	44	44	44	44
Mean	15.13	20.22	10.89	3.11	469
Stnd. Dev.	2.71	3.65	2.34	1.22	84
Median	15.80	21.00	11.20	3.00	491
Maximum	18.80	27.00	16.00	6.40	586
Minimum	8.70	10.30	4.40	1.00	269
Range	10.10	16.70	11.60	5.40	317

Table 4.–Pearson-product moment correlation matrix of temperature summaries. Bold indicates statistically significant at P<0.05.

	Annual					Winter					Summer					February					July				
	Mean	Max.	Min.	Flux	ATU	Mean	Max.	Min.	Flux	ATU	Mean	Max.	Min.	Flux	ATU	Mean	Max.	Min.	Flux	ATU	Mean	Max.	Min.	Flux	ATU
Annual																									
Mean	1.00																								
Max.	**0.67**	1.00																							
Min.	-0.11	**-0.58**	1.00																						
Flux	**0.36**	**0.52**	-0.27	1.00																					
ATU	**1.00**	**0.66**	-0.10	**0.35**	1.00																				
Winter																									
Mean	**0.36**	-0.28	**0.54**	0.03	**0.38**	1.00																			
Max.	**0.59**	**0.44**	-0.17	0.28	**0.58**	0.31	1.00																		
Min.	-0.10	**-0.58**	**1.00**	-0.27	-0.09	**0.54**	-0.16	1.00																	
Flux	0.07	-0.08	0.03	**0.67**	0.06	0.32	0.14	0.03	1.00																
ATU	**0.36**	-0.28	**0.54**	0.02	**0.39**	**1.00**	0.30	**0.54**	0.32	1.00															
Summer																									
Mean	**0.61**	**0.86**	**-0.55**	0.31	**0.61**	**-0.51**	0.25	**-0.55**	-0.22	**-0.51**	1.00														
Max.	**0.63**	**0.97**	**-0.56**	**0.50**	**0.59**	-0.26	**0.35**	**-0.56**	-0.07	-0.26	**0.81**	1.00													
Min.	0.09	-0.12	**0.42**	-0.07	0.10	0.11	-0.14	**0.41**	-0.10	0.10	0.02	-0.16	1.00												
Flux	**0.42**	**0.75**	**-0.42**	**0.87**	**0.41**	-0.20	0.28	**-0.42**	0.23	-0.21	**0.56**	**0.71**	-0.05	1.00											
ATU	**0.61**	**0.85**	**-0.55**	0.31	**0.59**	**-0.51**	0.24	**-0.55**	-0.22	**-0.51**	**1.00**	**0.80**	0.02	**0.57**	1.00										
February																									
Mean	0.16	**-0.43**	**0.61**	-0.08	0.19	**0.86**	-0.01	**0.61**	0.29	**0.87**	**-0.56**	**-0.40**	0.20	-0.31	**-0.56**	1.00									
Max.	0.32	-0.19	**0.39**	0.13	**0.35**	**0.83**	0.19	**0.39**	**0.33**	**0.83**	**-0.38**	-0.18	0.15	-0.06	**-0.39**	**0.90**	1.00								
Min.	0.00	**-0.54**	**0.88**	-0.22	0.02	**0.67**	-0.13	**0.88**	0.09	**0.67**	**-0.56**	**-0.53**	**0.42**	**-0.38**	**-0.56**	**0.79**	**0.57**	1.00							
Flux	-0.17	-0.32	0.18	0.31	-0.18	0.31	-0.06	0.18	**0.82**	0.31	**-0.42**	-0.28	-0.22	-0.13	**-0.42**	**0.37**	0.30	0.17	1.00						
ATU	0.16	**-0.43**	**0.61**	-0.07	0.19	**0.87**	-0.00	**0.61**	0.30	**0.87**	**-0.56**	**-0.40**	0.20	-0.31	**-0.56**	**1.00**	**0.90**	**0.79**	**0.37**	1.00					
July																									
Mean	**0.64**	**0.91**	**-0.64**	**0.41**	**0.62**	**-0.35**	**0.35**	**-0.63**	-0.12	**-0.35**	**0.91**	**0.87**	-0.13	**0.63**	**0.91**	**-0.52**	-0.32	**-0.59**	**-0.34**	**-0.52**	1.00				
Max.	**0.53**	**0.92**	**-0.59**	**0.47**	**0.51**	**-0.33**	0.24	**-0.58**	-0.08	**-0.33**	**0.77**	**0.95**	-0.19	0.68	**0.77**	**-0.48**	-0.29	**-0.57**	-0.26	**-0.48**	**0.86**	1.00			
Min.	**0.49**	**0.64**	**-0.47**	0.11	**0.48**	**-0.33**	0.21	**-0.46**	-0.19	**-0.33**	**0.78**	**0.56**	-0.07	0.29	**0.78**	**-0.39**	-0.26	**-0.43**	**-0.33**	**-0.39**	**0.80**	**0.49**	1.00		
Flux	**0.33**	**0.69**	**-0.40**	**0.83**	0.32	-0.22	0.17	**-0.40**	0.21	-0.22	**0.49**	**0.66**	-0.04	**0.95**	**0.50**	-0.30	-0.07	**-0.37**	-0.08	-0.30	**0.58**	**0.67**	0.21	1.00	
ATU	**0.64**	**0.92**	**-0.64**	**0.41**	**0.62**	**-0.35**	**0.34**	**-0.63**	-0.11	**-0.35**	**0.91**	**0.87**	-0.13	**0.63**	**0.91**	**-0.51**	-0.32	**-0.59**	**-0.34**	**-0.51**	**1.00**	**0.85**	**0.80**	**0.58**	1.00

Table 5.–Results of principal components analysis of temperature summaries from 17 study sites, 1993-95. Numbers in lower panel are coefficients of variables for each principle component (PCAs). Only complete annual records were used in this analysis which is based on the covariance matrix (N=34).

Component	Eigen value	% Variance explained
PCA1	212357.101	78.6
PCA2	57216.344	21.2
PCA3	272.641	0.1
PCA4	184.191	0.1
PCA5	5.497	0.0

Variable	PCA1	PCA2	PCA3	PCA4	PCA5
Annual					
Mean	-3.3900E-06	6.6600E-06	1.9500E-06	-1.1690E-05	1.0919E-03
Max.	-1.6420E-05	-4.3200E-06	1.3495E-04	-2.2728E-03	1.8673E-02
Min.	2.4500E-06	1.0190E-05	-3.7345E-04	1.1410E-03	-2.9619E-02
Flux	-1.3400E-06	3.3000E-06	2.4889E-04	-1.3207E-03	5.8982E-03
ATU	-1.2252E-03	2.4447E-03	-2.3662E-03	4.8599E-03	-2.5414E-03
Winter					
Mean	2.5300E-06	1.8050E-05	-4.5340E-05	-2.1950E-05	1.5154E-03
Max.	-7.2400E-06	1.6560E-05	-3.6887E-03	-1.2630E-03	3.9712E-01
Min.	2.4500E-06	1.0190E-05	-3.7345E-04	1.1410E-03	-2.9619E-02
Flux	2.7000E-07	5.2600E-06	5.2454E-04	-1.1433E-03	3.0117E-02
ATU	4.5609E-04	3.2490E-03	-5.8351E-03	-7.0231E-03	-3.2218E-03
Summer					
Mean	-9.1000E-06	-4.3000E-06	-2.8600E-06	8.7310E-05	3.5644E-04
Max.	-1.6230E-05	-4.9600E-06	3.5569E-04	-2.2996E-03	-2.1257E-02
Min.	-3.0000E-08	6.8200E-06	-1.7483E-03	2.3735E-03	-2.7914E-02
Flux	-2.9700E-06	1.2100E-06	-2.3320E-05	-1.5265E-03	-1.7267E-02
ATU	-1.6813E-03	-8.0429E-04	3.4836E-03	1.1860E-02	2.2964E-03
February					
Mean	4.4500E-06	1.7030E-05	2.1151E-03	1.8217E-04	1.1696E-04
Max.	3.8100E-06	2.2240E-05	1.0896E-03	-1.3494E-03	1.1112E-02
Min.	2.5700E-06	9.4600E-06	4.9678E-04	9.1646E-04	-1.8532E-02
Flux	2.3700E-06	9.2200E-06	2.1161E-03	-2.3742E-03	7.9814E-02
ATU	1.2463E-04	4.8119E-04	5.9717E-02	4.6052E-03	2.0578E-02
July					
Mean	-1.2740E-05	-8.2100E-06	1.4575E-04	-2.3301E-03	-2.4264E-04
Max.	-1.5530E-05	-1.2700E-05	2.2456E-04	-4.2277E-03	-8.7236E-02
Min.	-8.4100E-06	-6.8000E-07	-4.6520E-05	-1.3440E-04	4.2313E-02
Flux	-3.3800E-06	7.4000E-07	3.0046E-04	-2.7710E-03	-5.4344E-02
ATU	-3.9558E-04	-2.5416E-04	4.6870E-03	-7.1619E-02	-3.0683E-03
Constant	7.3137E+00	-6.9953E+00	-2.9132E+00	-3.5665E+00	1.2189E+00

Table 6.–Pearson product-moment correlation matrices of primary and secondary principal components with trout population characteristics and temperature summaries. ATU=sum of mean daily temperatures. Bold indicates significant at P≤0.05(*) or P≤0.01(**).

Variable	PCA1	PCA2
PCA1	1.00	
PCA2	0.01	1.00
Annual		
Mean	**-0.76 ****	**0.63 ****
Maximum	**-0.88 ****	-0.01
Minimum	**0.49 ****	**0.41 ****
Flux	**-0.36 ***	0.12
ATU	**-0.75 ****	**0.65 ****
Winter		
Mean	0.32	**0.95****
Maximum	**-0.36 ***	**0.45 ****
Minimum	**0.48 ****	**0.42 ****
Flux	0.16	0.28
ATU	0.32	**0.95 ****
Summer		
Mean	**-0.98 ****	-0.22
Maximum	**-0.83 ****	-0.02
Minimum	-0.04	0.12
Flux	**-0.57 ****	-0.04
ATU	**-0.98 ****	-0.23
February		
Mean	**0.41 ***	**0.78 ****
Maximum	0.23	**0.80 ****
Minimum	**0.46 ****	**0.57 ****
Flux	**0.39 ***	0.19
ATU	**0.42 ***	**0.78 ****
July		
Mean	**-0.92 ****	-0.09
Maximum	**-0.77 ****	-0.11
Minimum	**-0.77 ****	-0.12
Flux	**-0.50 ****	-0.08
ATU	**-0.91 ****	-0.09
Brook trout		
Density (number/ha)	**0.41 ***	-0.06
Standing stock (kg/ha)	0.27	-0.07
Growth rate (g/day)	**-0.57 ****	0.09
Brown trout		
Density (number/ha)	-0.14	0.04
Standing stock (kg/ha)	-0.19	0.06
Growth rate (g/day)	**-0.69 ****	-0.23

Table 7.–Juvenile brook trout densities at study sites as mean values for all sampling periods, 1993-95. Trout were defined as juvenile if they were ≤100 mm total length. (Au) = Au Sable River site.

Site	Numerical density (number/ha) Mean	Numerical density (number/ha) Stn. Dev.	Standing stock (kg/ha) Mean	Standing stock (kg/ha) Stn. Dev.	N (years)
Antrim Creek	463	408	1.44	1.41	3
Belanger Creek	245	290	1.37	1.59	3
Big Creek	11	16	0.06	0.08	2
Chase Bridge (Au)	219	267	1.64	1.88	3
Dam Four (Au)	3228	787	18.79	5.45	3
Gilchrist Creek	105	na	0.96	na	1
Hunt Creek	4598	2141	27.70	9.34	3
Irontone Springs	1162	981	4.66	4.68	3
Monroe Creek	903	180	4.16	0.48	3
Rapid River	5776	309	23.84	2.78	3
Roaring Brook	2269	624	7.30	2.15	3
SB Pigeon River	1669	776	10.29	4.34	3
SB Spring Brook	1199	209	3.98	0.44	3
Stephans Bridge (Au)	912	229	6.01	1.75	3
Stover Creek	924	na	4.71	na	1
Twin Bridges (Au)	1234	317	8.19	1.17	3
Wa Wa Sum (Au)	838	95	5.94	1.30	3

Table 8.–Juvenile brown trout densities at study sites as mean values for all sampling periods, 1993-95. Trout were defined as juvenile if they were ≤ 100 mm total length. (Au) = Au Sable River site.

Site	Numerical density (number/ha)		Standing stock (kg/ha)		N (years)
	Mean	Stn. Dev.	Mean	Stn. Dev.	
Antrim Creek	0	0	0.00	0.00	3
Belanger Creek	3307	1491	18.91	7.46	3
Big Creek	2247	555	12.79	4.78	2
Chase Bridge (Au)	428	181	3.47	1.21	3
Dam Four (Au)	735	237	5.41	1.72	3
Gilchrist Creek	535	na	4.01	na	1
Hunt Creek	10	18	0.05	0.09	3
Irontone Springs	0	0	0.00	0.00	3
Monroe Creek	575	756	3.60	4.99	3
Rapid River	0	0	0.00	0.00	3
Roaring Brook	0	0	0.00	0.00	3
SB Pigeon River	0	0	0.00	0.00	3
SB Spring Brook	0	0	0.00	0.00	3
Stephans Bridge (Au)	751	272	6.26	1.97	3
Stover Creek	0	na	0.00	na	1
Twin Bridges (Au)	418	74	3.37	0.49	3
Wa Wa Sum (Au)	255	85	1.86	0.66	3

Table 9.–Pooled juvenile (TL≤100 mm) brook trout population characteristics from 17 sites sampled in 1993-95. Note: Juvenile brook trout were not present at some sites during certain years, some sites were not sampled each year, and juvenile brown trout were present at 8 sites.

	Growth rate (g/day)	Wet weight (g)	Density (number/ha)	Standing stock (kg/ha)
All sites				
N	38	38	40	40
Mean	0.0170	5.19	1611	7.90
Standard deviation	0.0076	1.77	1766	8.67
Median	0.0151	5.25	926	4.70
Maximum	0.0311	9.10	6960	38.10
Minimum	0.0078	2.70	0	0.00
Range	0.0233	6.40	6960	38.10
Sites without brown trout				
N	21	21	21	21
Mean	0.0125	4.19	2298	10.35
Standard deviation	0.0052	1.40	2040	10.09
Median	0.0105	3.70	1559	6.16
Maximum	0.0273	7.20	6960	38.10
Minimum	0.0078	2.70	89	0.25
Range	0.0195	4.50	6871	37.85

Table 10.–Pooled juvenile (TL≤100 mm) brown trout population characteristics from 17 sites sampled in 1993-95. Note: Juvenile brown trout were collected at 10 different sites. They were not present at all of these sites each year, and not all sites were sampled each year.

			Sites with brown trout		All sites	
	Growth rate (g/day)	Wet weight (g)	Density (number/ha)	Standing stock (kg/ha)	Density (number/ha)	Standing stock (kg/ha)
N	19	19	19	19	40	40
Mean	0.0230	6.67	1086	6.70	516	3.18
Stnd. Dev.	0.0069	1.20	1284	7.08	1031	5.88
Median	0.0218	7.00	558	4.25	0	0.00
Maximum	0.0317	8.60	4997	27.50	4997	27.50
Minimum	0.0128	4.50	31	0.16	0	0.00
Range	0.0189	4.10	4966	27.34	4997	27.50

Table 11.–Pearson product-moment correlation matrix among juvenile trout population characteristics based on 17 sites sampled in 1993-95. Note: Not all sites were sampled each year. Bold indicates significant at P≤0.05(*) or P≤0.01(**).

	Brook trout			Brown trout		
	Density (number/ha)	Standing stock (kg/ha)	Growth (g/day)	Density (number/ha)	Standing stock (kg/ha)	Growth (g/day)
Brook trout						
Density	1.00					
Standing stock	**0.95 ****	1.00				
Growth	-0.12	0.10	1.00			
Brown trout						
Density	-0.34	-0.32	0.11	1.00		
Standing stock	-0.36	-0.33	0.17	**0.99 ****	1.00	
Growth	0.12	0.21	**0.88 ****	**-0.52 ***	**-0.46 ***	1.00

Table 12.–Pearson product-moment correlations between juvenile trout population characteristics and temperature summaries from 17 sites sampled in 1993-95. Note: Not all sites were sampled each year. ATU= sum of mean daily temperatures. Bold indicates significant at P≤0.05(*) or P≤0.01(**).

	Brook trout			Brown trout		
Temperature summary	Growth (g/day)	Density (number/ha)	Standing stock (kg/ha)	Growth (g/day)	Density (number/ha)	Standing stock (kg/ha)
Annual						
Mean	**0.52 ****	**-0.36 ***	-0.25	0.28	0.15	0.20
Max.	**0.67 ****	**-0.37 ***	-0.21	**0.66 ****	0.17	0.22
Min.	-0.24	0.19	0.12	0.01	-0.18	-0.21
Flux	**0.56 ****	0.23	**0.38 ***	0.20	0.11	0.14
ATU	**0.49 ****	**-0.35 ***	-0.25	0.23	0.14	0.18
Winter						
Mean	-0.08	0.07	0.02	-0.36	-0.01	-0.01
Max.	**0.42 ****	-0.18	-0.10	0.17	0.28	**0.34 ***
Min.	-0.25	0.18	0.11	0.01	-0.18	-0.21
Flux	0.07	**0.33 ***	**0.33 ***	-0.12	0.15	0.15
ATU	-0.09	0.06	0.01	-0.36	-0.01	-0.01
Summer						
Mean	**0.53 ****	**-0.39 ***	-0.25	**0.72 ****	0.13	0.16
Max.	**0.60 ****	**-0.40 ***	-0.24	**0.51 ****	0.17	0.21
Min.	0.06	0.06	0.04	0.27	-0.31	**-0.36 ***
Flux	**0.66 ****	0.09	0.28	0.36	0.06	0.09
ATU	**0.53 ****	**-0.39 ***	-0.25	**0.72 ****	0.12	0.16
February						
Mean	-0.28	0.14	0.06	-0.44	-0.19	-0.22
Max.	-0.11	0.17	0.14	-0.27	-0.16	-0.17
Min.	-0.23	0.09	0.03	-0.25	-0.23	-0.26
Flux	-0.20	0.26	0.18	-0.28	0.08	0.07
ATU	-0.29	0.13	0.06	-0.43	-0.19	-0.22
July						
Mean	**0.63 ****	**-0.42 ****	-0.26	**0.73 ****	0.21	0.27
Max.	**0.54 ****	**-0.34 ***	-0.18	0.35	0.20	0.23
Min.	**0.48 ****	**-0.41 ****	-0.31	**0.61 ****	0.04	0.11
Flux	**0.67 ****	0.18	**0.35 ***	0.41	0.02	0.05
ATU	**0.63 ****	**-0.42 ****	-0.26	**0.72 ****	0.21	0.26

Table 13.–Results of multiple linear regressions of growth (g/day), density (number/ha), and standing stock (kg/ha) of juvenile trout with the two temperature principal components (PCAs). Note: Bolded F-statistics are statistically significant. (SR) = square root transformation.

Dependent variable	Independent variables	Relationship (+/-)	F-statistic	P-value	d.f.	R^2	Adjusted R^2
Brook trout							
Growth	PCA1	-	**8.81**	<0.001	35	0.335	0.297
	PCA2	+					
Density	PCA1	+	**3.91**	<0.05	37	0.175	0.130
	PCA2	-					
Standing crop	PCA1	+	1.58	>0.10	37	0.079	0.029
	PCA2	-					
Brook trout without brown trout							
Growth	PCA1	-	0.24	>0.75	18	0.026	-0.083
	PCA2	-					
Density (SR)	PCA1	+	1.48	>0.25	18	0.141	0.046
	PCA2	+					
Standing crop (SR)	PCA1	+	0.59	>0.50	18	0.061	-0.043
	PCA2	+					
Brown trout							
Growth	PCA1	-	**9.19**	<0.001	16	0.535	0.476
	PCA2	-					
Density (SR)	PCA1	+	3.02	>0.05	37	0.140	0.094
	PCA2	-					
Standing crop (SR)	PCA1	-	**3.82**	<0.05	37	0.171	0.126
	PCA2	+					

Table 14.–Results of multiple linear regressions of growth (g/day) of juvenile trout with temperature summaries (PCAs) and juvenile trout densities (number/ha). Note: Bolded F-statistics and variables are statistically significant for the model. (SR) = square root transformation.

Dependent variable	Independent variables	Coefficient	P-value	F-statistic	P-value	d.f.	R^2	Adjusted R^2
Brook trout growth (SR)	**PCA1**	-0.01663	0.001	**5.67**	<0.005	4/33	0.407	0.335
	PCA2	0.00154	0.548					
	Brook density (SR)	0.00039	0.108					
	Brown density (SR)	0.00048	0.114					
	Constant	0.10807	<0.001					
Brook trout growth (SR) (no browns)	PCA1	-0.00716	0.244	1.87	>0.100	3/17	0.248	0.115
	PCA2	-0.00154	0.677					
	Brook density (SR)	0.00054	0.039					
	Constant	0.09103	<0.001					
Brown trout growth (SR)	**PCA1**	-0.01997	0.012	**4.65**	<0.025	4/14	0.571	0.448
	PCA2	-0.00408	0.132					
	Brook density (SR)	-0.000028	0.931					
	Brown density (SR)	-0.00036	0.287					
	Constant	0.15278	<0.001					

Table 15.–Results of six multiple linear regressions of growth (g/day) of juvenile trout with summer and winter mean temperature summaries and juvenile trout densities (number/ha). Note: Bolded F-statistics and variables are statistically significant for the model. (SR) = square root transformation.

Dependent variable	Independent variables	Coefficient	P-value	F-statistic	P-value	d.f.	R^2	Adjusted R^2
Brook trout growth (SR)	**summer mean**	0.00953	<0.001	**8.58**	<0.005	2/35	0.329	0.291
	winter mean	0.00449	0.108					
	constant	-0.00689	0.846					
Brook trout growth (SR)	**summer mean**	0.00224	0.004	0.26	>0.75	2/18	0.028	-0.080
(no browns)	winter mean	0.00064	0.888					
	constant	0.08319	0.172					
Brook trout growth (SR)	**summer mean**	0.00960	0.001	**5.64**	<0.005	4/33	0.406	0.334
	winter mean	0.00409	0.151					
	brook density (SR)	0.00397	0.104					
	brown density (SR)	0.00047	0.099					
	constant	-0.02607	0.541					
Brook trout growth (SR)	summer mean	0.00420	0.264	1.91	>0.10	3/17	0.252	0.120
(no browns)	winter mean	0.00037	0.929					
	brook density (SR)	0.00054	0.038					
	constant	0.03739	0.512					
Brown trout growth (SR)	**summer mean**	0.01049	0.023	**4.59**	<0.05	2/12	0.433	0.339
	winter mean	-0.00343	0.906					
	constant	0.00743	0.902					
Brown trout growth (SR)	**summer mean**	0.00971	0.029	**4.46**	<0.025	4/14	0.560	0.434
	winter mean	-0.00153	0.609					
	brook density (SR)	-0.00003	0.938					
	brown density (SR)	-0.00036	0.288					
	constant	0.03649	0.598					

Table 16.–Results of simple linear regressions of growth rate (g/day) of juvenile trout with simple water temperature summaries. Note: Bolded F-statistics and variables are statistically significant for the model. (SR) = square root transformation.

Dependent variable	Independent variable	Coefficient	P-value	F-statistic	P-value	d.f.	r^2
Brook trout growth (SR)	**July flux**	0.01608	<0.001	**33.6**	<0.001	36	0.4820
	constant	0.07827	<0.001				
Brown trout growth (SR)	**July mean**	0.01169	<0.001	**19.3**	<0.001	17	0.5310
	constant	-0.04716	0.310				

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