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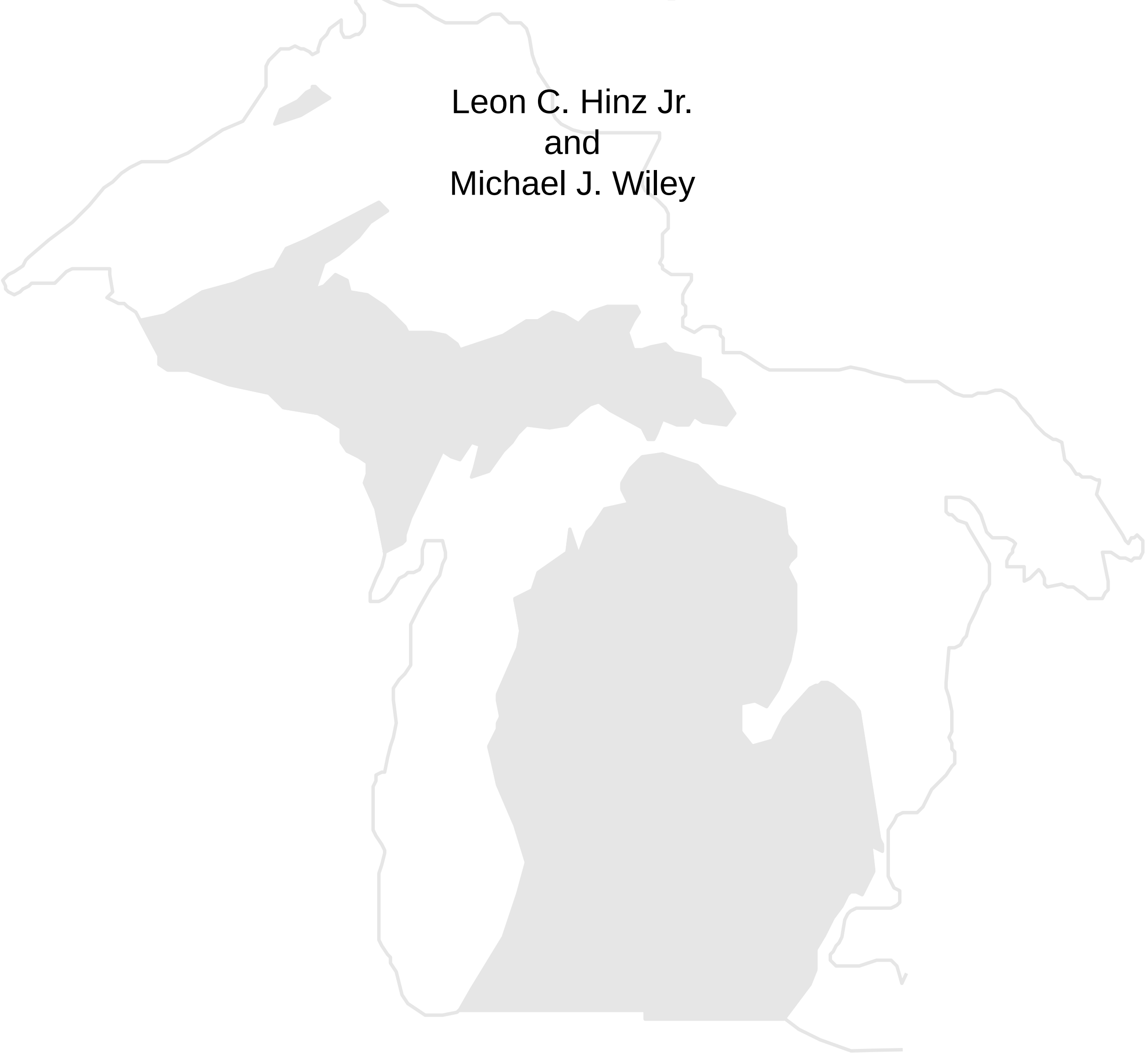

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# Growth and Production of Juvenile Trout in Michigan Streams: Influence of Potential Ration and Temperature

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*Abstract.*–Twelve streams in northern lower Michigan were studied over a 3-year period to determine the influence of temperature and macroinvertebrate standing crop on growth and production of juvenile trout (*Salvelinus fontinalis* and *Salmo trutta*). Thermal conditions were typical for small streams in the glacial outwash regions of Michigan, which are heavily influenced by ground water. Macroinvertebrate community compositions were found to differ between sites although dominant taxa were similar. Total macroinvertebrate standing stock was correlated with several different measures of temperature including mean daily summer temperature, suggesting greater macroinvertebrate densities at higher temperatures. Observed young-of-the-year (YOY) brook trout growth rates varied from 0.0084 to 0.0266 g/day (a factor of >3x). Brown trout growth rates ranged from 0.0158 to 0.0218, but YOY brown trout were absent from 7 of 12 sites. Results indicated that overall benthic prey availability was more variable over time than was temperature or YOY growth performance. YOY brook trout growth was significantly correlated with total abundance of adult trout (kg/ha; all species combined). We developed several multiple regression models for predicting growth of juvenile brook trout in small ground water streams. The best-fit model included thermal, biological and nutrient (total phosphorus) variables as predictors ($R^2$ adj. = 0.86).

We also developed a causal path model with temperature and macroinvertebrate components to examine the underlying causes of juvenile brook trout growth rate and to estimate the direct and indirect effects of temperature on growth. In this model temperature was the strongest factor affecting variation in juvenile brook trout growth rate, having about a 50% greater effect on growth than all ration variables combined. However, indirect effects of temperature acting on growth rate through the ration variables accounted for approximately half of the total temperature effect. Ration effects on trout growth rate were also statistically significant, with the predator taxa being slightly more important than filter-feeding primary consumers. Biomass of both groups increased with increasing temperature and together provided the basis for temperature's indirect effect on trout. Management applications to small ground water fed trout streams are discussed in relation to the results of this study.

Temperature and ration are two major factors influencing the growth of fish (Brett 1979, Diana 1996). In both laboratory studies and in natural trout streams, higher growth rates occur with warmer water (e.g., Johnson et al 1992), and growth declines in cooler water (Cunjak and Power 1987; Cumjak et al 1987). Detailed relationships between ration and growth rate have been developed by Elliott (1994) for brown trout. In Michigan's Pigeon River Cooper (1953) found a positive correlation with abundance of food organisms and brook trout growth rate**.** These studies and others (e.g., Ensign et al 1990, Nicieza and Metcalfe 1997), suggest that food availability is a particularly important factor in determining growth of salmonids. However, both spatial and temporal variability of food organism abundance in trout streams can be high (Leonard 1939; Needham and Usinger 1956, Wiley et al 1997). This high variability may confound the effects of temperature on trout growth by altering potential ration in field settings. Further, there is little reason to believe that in natural stream ecosystems ration production and thermal regime are totally independent parameters. Thus the extrapolation from controlled laboratory studies of ration and temperature effects on growth, to predictions of populations' responses in the field may be difficult. Such predictions, however, are of interest both to trout population managers, and to workers interested in estimating the potential effects of climate change.

In a recent study, we evaluated the influence of temperature on the growth of juvenile trout at 17 sites in northern Lower Michigan (Hinz and Wiley 1997). We were able to explain a large fraction of the variance in the growth rate of juvenile brook trout *Salvelinus fontinalis* (48.2%) and juvenile brown trout Salmo *trutta* (53.1%) using linear regression models with a single predictive variable (either mean daily temperature fluctuation during July for brook trout or July mean daily temperature for brown trout). While these models are encouraging, they do not account for approximately half of the variation.

The major objective of this study was to examine the relationships between temperature regime, macroinvertebrate prey populations, and the growth and production of juvenile trout in cold water streams. Many of the streams included in our previous study (Hinz and Wiley 1997) have experienced wide fluctuations in macroinvertebrate abundance associated with parasites of dominant caddisfly populations (Kohler and Wiley 1994, 1997; Wiley et al 1997). If the potentially available ration at a site differs dramatically from year to year (or even seasonally), then thermal effects on growth may be masked. In order to improve our understanding of the factors influencing growth and production of juvenile trout, we estimated growth rate and production of juvenile brook trout and juvenile brown trout in 12 small streams in the northern Lower Peninsula of Michigan over a period of three years. We supplemented these data with concurrent measurements of temperature and macroinvertebrate standing crop. These data are used in this report to explore the covariation occurring in Michigan streams between juvenile brook trout production, macroinvertebrate prey availability, and in-stream thermal regime.

## Methods

The twelve study 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). 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 (1994-95) set at measurement intervals of 96 minutes (except Hunt Creek with a measurement interval of 60 minutes). Measurements collected at each site with the thermographic recorders were summarized into daily and monthly mean, maximum, and minimum temperatures; 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.

Chemical parameters were estimated using standard methods (Eaton et al 1995) from water samples collected bimonthly during the summer of 1996. We measured alkalinity, total phosphorus, soluble reactive phosphate, total inorganic nitrogen, nitrate-nitrite nitrogen, ammonia, and pH from each sample and averaged the values for each month. Mean values for a given site were used in the analyses.

Quarterly invertebrate sampling (February, May, August, November) consisted of removing four clusters of five rocks within randomly selected one square foot areas of stream bottom during each year 1993-95. Rocks were collected after a small net (250 micron mesh) was placed downstream from each target rock. The rocks and net contents were then placed in a whirl-pac bag, preserved with 5% formalin and returned to the laboratory for analysis. Samples from two of the four sampling dates each year were used in the analysis (one summer and one winter). These samples were analyzed for stone surface area (using image analysis), macroinvertebrate density and biomass by species. Rocks were scraped, washed, and sorted at 10x under a dissecting microscope. Organisms were identified to species when possible and their lengths converted to biomass using species-specific length-mass relationships. Quarterly rock collections were supplemented in late winter (February) at each of the survey sites by the use of a modified Hess sampler (except when ice precluded sampling). Six to ten samples were collected by random placement of the sampler, working upstream through the reach from one side of the stream to the other. Invertebrate predators and other large macroinvertebrates were preserved and returned to the laboratory for analysis (as described above for rock samples). Macroinvertebrates were summarized as functional feeding groups (Merritt & Cummins 1996) and family groups for analysis in this study.

Fish sampling was conducted in December of each year when possible (ice cover precluded sampling at some sites in some years), except at Hunt Creek where late September sampling occurred. Sampling included a 3-pass removal estimate (Zippen 1958) or a mark-recapture estimate (Hunt Creek only) 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. 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.

Juvenile status for trout was based on two lines of evidence. Trout were aged from scale samples taken at the study sites. Only age 0 trout were found to be ≤100 mm (3.94 inches) at these sites. Secondly, in a fall study of Hunt Creek, one of our study streams by McFadden et al (1967) found no mature brook trout <5 inches long and no age 1 trout <4 inches long. Therefore, trout were conservatively defined as juveniles for this study if their total length was ≤100 mm (3.94 inches) and they were age 0.

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. Gowing and Alexander (1980) found a strong and direct relationship between fall standing crop and annual production of stream salmonids (r=0.959, df=12). 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 juveniles (age 0).

Statistical analyses were performed using Data Desk (Velleman and Capehart 1995). Where necessary, variables were normalized using square root, natural logarithm or other transformations. We used Pearson product-moment correlation (r), simple linear regression (SLR), and multiple linear regression (MLR) to summarize the relationships between the variables. A combination of forward selection ($p < 0.05$) and backward elimination ($p > 0.10$) stepwise regression (SR) was used to develop predictive models for brook trout growth rates. Standard factorial ANOVA techniques were also used to partition the sum of squared deviations from the ANOVA table into components associated with inter-site spatial variation ($SS_{site}$) and regionally synchronous annual variation ($SS_{yr}$) and site-specific annual variation + error (see Wiley et al 1997). Path analysis was used to determine the relative magnitude of ration and temperature effects on the growth rate of juvenile brook trout, and to identify direct and indirect effects of temperature (Asher 1983, Sokal and Rohlf 1995).

## Results

### *Thermal Characteristics*

Thermal conditions were typical for small streams in glacial outwash regions of the Lower Peninsula of Michigan (Seelbach & Wiley 1997). Six sites averaged less than 2800 ATU per year (mean daily temperature 7.7 C) with an overall mean of 2854 ATU (annual mean daily temperature 7.8 C) for all sites during the study (Table 1). The maximum mean ATU (Monroe Creek 3283 ATU, mean daily temperature 9.0 C) was about 1.3 times greater than the minimum (Irontone Springs 2489 ATU, mean daily temperature 6.8 C). Maximum recorded temperature at individual sites varied between 14.0 C (South Branch Spring Brook) and 24.0 C (Big Creek and Monroe Creek). Minimum recorded temperatures ranged from a low at Antrim Creek of –2.4 C to a high of 2.0 C at the South Branch of Spring Brook. The overall mean daily winter temperature was 3.8 C with a low of 1.3 C at Antrim Creek and a high of 5.9 C at Roaring Brook. Summer mean daily temperature (overall mean 11.8 C) ranged from 8.7 C at the South Branch of Spring Brook to 14.4 C at Antrim Creek.

While ATU (or annual mean daily temperature) can be a useful measure for between site comparisons it ignores potentially important temporal variation. Belanger Creek (2889 ATU) and Roaring Brook (2901 ATU) each had an annual mean daily temperature of 7.9 C and differed by an average of only 12 ATU per year (Table 1). However, winter and summer mean daily temperatures are over 2 C different between the sites with Belanger Creek having lower winter (3.7 C vs. 5.9 C) and higher summer (12.1 C vs. 10.0 C) temperatures than Roaring Brook. At shorter time intervals these differences are even more striking. The July temperature summaries can be used to illustrate these differences. Belanger Creek had a higher mean daily temperature (15.8 C vs. 11.2 C), a higher maximum temperature (20.0 C vs. 15.4 C) and a greater mean daily temperature fluctuation (2.2 C vs. 1.2 C) than Roaring Brook. These results suggest that a single summary variable may not be adequate for describing the thermal character of trout streams.

### *Chemical Characteristics*

Alkalinity ranged from 160 mg $CaCO_3$/l to 302 mg $CaCO_3$/l between the study sites (Table 2). Total phosphorus (TP) was highest at Belanger Creek (40 ppb) and lowest at the South Branch of Spring Brook (8 ppb). The overall mean for total inorganic nitrogen (TIN) was 609 ppb, and the average of the pH measurements was 7.7 for all sites.

### *Macroinvertebrate Characteristics*

The Chironomidae were numerically the most abundant taxonomic group with an average of more than 15,000 individuals collected per square meter from each site and date (Table 3). *Protoptila* sp. (3,146/$m^2$) and the Baetidae (2,896/$m^2$) were the next most abundant macroinvertebrates. Predators were dominated by three species of *Rhyacophila* (5/$m^2$) and two species of *Isogenoides* (3/$m^2$). Standing stocks of non-predatory macroinvertebrates consisted primarily of filter feeders (931 mg dry mass/$m^2$ (mgdw/m)) mainly Hydropsychidae (479 mgdw/m) and Simuliidae (301 mgdw/m) and Grazers (987 mgdw/m) primarily *Glossosoma* (245 mgdw/m) and *Protoptila* (212 mgdw/m). Standing stocks of macroinvertebrate predators (142 mgdw/m) were mainly *Isogenoides* (53 mgdw/m) and *Rhyacophila* (36 mgdw/m).

The study sites varied in their macroinvertebrate compositions. The Hydropsychidae ranged from 4.9 mgdw/m at the South Branch of Spring Brook to 1746.1 mgdw/m at the South Branch of the Pigeon River (Table 4). Big Creek had the highest blackfly density (967.8 mgdw/m) and Stover Creek the lowest (33.6 mgdw/m). Larvae of the genus *Glossosoma* made up the majority of the grazing biomass with a mean of 245.4 mgdw/m over all sites. Baetidae density was lowest at Monroe Creek (24.9 mgdw/m) and highest at the South Branch of Spring Brook (634.4 mgdw/m).

Macroinvertebrate predators also differed between the sites. Overall predator densities varied between 3.4 mgdw/m at Roaring Brook to 336.4 mgdw/m at Monroe Creek (Table 5). *Isogenoides* density was highest at Belanger Creek (120.4 mgdw/m) and *Rhyacophila* density was greatest at the South Branch of Spring Brook (95.4 mgdw/m).

Total macroinvertebrate standing stock was significantly correlated with pooled non-predatory macroinvertebrates (r=0.997), grazers (r=0.829), and filter-feeders (r=0.825) (Table 6). In general non-predatory trophic guilds and taxa were positively correlated with each other suggesting that some sites were more favorable than others. There were no significant correlations between total macroinvertebrate predator biomass and the other functional groups.

### *Trout Population Characteristics*

Juvenile brook trout occurred at all twelve of the study sites. Densities varied well over a hundredfold from 11/ha (Big Creek) to 5,776/ha (Rapid River) (Table 7). Mean standing stock for all sites during the study was 8.39 kg/ha (188 mgdw/m) with a low of 0.06 kg/ha (1 mgdw/m) at Big Creek and a high of 27.7 kg/ha (620 mgdw/m) at Hunt Creek.

Mean size of juvenile brook trout during the study was 4.6 grams wet weight (1.03 g dry mass (gdm)) (Table 8). Sizes ranged from 2.9 g (0.65 gdm) at Antrim Creek to 9.1 g (2.04 gdm) at Gilchrist Creek. Growth rates varied from a low of 0.0095 gram wet weight/day (2.1 mg dry mass/day) at the South Branch of Spring Brook to a high of 0.0266 g/day (6.0 mg dry mass/day) at Gilchrist Creek.

Juvenile brown trout were collected at only five of the twelve study sites. Greatest abundances were observed at Belanger Creek (3,307/ha and 18.91 kg/ha (420 mgdw/m)) and Big Creek (2,247/ha and 12.79 kg/ha (290 mgdw/m)) (Table 9).

The largest average sized juvenile brown trout were collected at Gilchrist Creek (7.5 grams wet weight, 1.7 gdm) (Table 10). Overall mean growth rate for juvenile brown trout was 0.0170 g/day (3.8 mg dry mass/day). Growth rates ranged from 0.0158 g/day (3.5 mg dry mass/day) at Big Creek and Monroe Creek to a high at Gilchrist Creek of 0.0218 g/day (4.9 mg dry mass/day).

Juvenile trout growth was strongly and positively correlated between species (r=0.723) suggesting that some sites were more favorable for growth (Table 11). Brook trout growth was also positively correlated with standing stock of juvenile brook trout (r=0.381) but not significantly correlated with standing stock of juvenile brown trout (r=0.177). Standing stocks between species were negatively correlated (r=-0.343) although this was heavily influenced by the absence of brown trout at many sites (Tables 9 and 11).

### *Temperature and Macroinvertebrates*

Annual maximum temperature (r=0.564), mean annual daily temperature fluctuation (r=0.390), and all the summer and July temperature summary parameters were significantly and positively correlated with total macroinvertebrate biomass per unit area (Table 6). Grazer biomass was significantly correlated with summer temperature fluctuation (r=0.391) and July temperature fluctuation (r=0.371), but none of the other temperature summary parameters. Filter-feeders were significantly and positively correlated with all of the summer and July temperature summaries and the annual maximum and temperature fluctuations. Biomass of total macroinvertebrate predators was not significantly correlated with any of the temperature summary statistics except for summer temperature fluctuation (r=0.378).

### *Temperature and Trout*

Growth in juvenile brook trout was found to be strongly and positively correlated with the daily fluctuation in temperature. Annual fluctuation (r=0.800), winter fluctuation (r=0.346), summer fluctuation (r=0.786), and July fluctuation (r=0.801) were all highly correlated with growth rate (Table 12). Trout growth and annual, summer and July maximum temperatures were also positively correlated.

Density of juvenile brook trout was most strongly and negatively correlated with mean daily temperature for the month of July (r=-0.408). The maximum temperature in July was the parameter most highly correlated with the production of juvenile brook trout (r=0.460), as measured by standing stock, of any of the thermal summary variables in this study.

There were no statistically significant correlations between juvenile brown trout growth rate and any of the thermal parameters used in this study (Table 12). Density and standing stock of juvenile brown trout each had significant correlations with the maximum temperature for the winter period (November 1-April 30); although making generalizations from these relationships must be done cautiously since juvenile brown trout were absent from many of the sites (Tables 9 and 12).

Since our earlier models explained 48.2% of the variance in juvenile brook trout growth and 53.1% of the variation in juvenile brown trout growth (Hinz and Wiley 1997), we used similar simple linear regression models as a starting point for analysis in this study. Mean daily July temperature fluctuation explained a larger fraction (65.1%) of the growth rate of brook trout in the present study but did not explain a statistically significant amount of the juvenile brown trout growth rate (Table 13). Therefore further analysis of growth rates and thermal parameters in this study was limited to juvenile brook trout.

Juvenile trout production was less well correlated to the temperature summary variables. Maximum July temperature was the most highly correlated variable (r=0.460) with juvenile brook trout production (Table 12). Brook trout were also positively correlated with annual (r=0.436) and summer (r=0.357) temperature fluctuations (Table 9). Since juvenile brown trout were restricted to only five sites few strong correlations were found between density or standing stocks and the thermal variables. The only significant correlation between juvenile brown trout production was with the maximum winter temperature (r=0.440) (Table 12).

### *Prey Biomass and Trout Growth*

*Rhyacophila* (a common predatory caddisfly) biomass (r=0.400) was the only macroinvertebrate parameter that was significantly correlated with brook trout growth rate (Table 11). Juvenile brook trout production (standing stock) was not significantly correlated with any of the macroinvertebrate summary parameters used in this study. Growth rate of brown trout had no significant correlations with the macroinvertebrate summary parameters. *Isogenoides* (a common predatory stonefly) biomass (r=0.435) was positively correlated with brown trout standing stock.

We used the ratio of macroinvertebrate predator to non-predator mass (*trophic ratio*) as an index of the energy transfer efficiency from primary consumers to their predators. The trophic ratio was positively correlated with juvenile brown trout standing stock (r=0.410), but none of the other trout growth or density parameters (Table 11).

### *Variance Structures*

The variance structures for juvenile brook trout growth rate, July mean temperature, and July daily temperature flux were similar (Figure 2). Spatial variation (constant inter-site differences) accounted for more than 90% of the total variance in each of these parameters and at least to 95% for temperature fluctuation and growth rate. Regionally coherent annual variation was low (<1-3%) as was site-specific annual variation (<8%). Site-specific dynamics appeared relatively more important in the macroinvertebrate data. Annual within-site variation comprised 18% of the overall variance for total macroinvertebrate standing stock and 38% for *Glossosoma* standing crop. These results indicate that for Michigan brook trout populations, ration is more variable over time within sites than temperature. Ration variability may therefore be responsible for much of the observed year to year (temporal) variation in brook trout growth, while thermal regime may be the primary factor influencing the average growth differences that occur between sites.

### *Path Analysis*

We developed a causal path model with temperature and macroinvertebrate components to examine the underlying causes of juvenile brook trout growth rate and to estimate the direct and indirect effects of temperature on growth (Figure 3). The path diagram included two primary consumer groups (grazers and filter-feeders) and macroinvertebrate predators (pooled *Isogenoides* and *Rhyacophila* density). A single thermal variable (mean daily July temperature fluctuation) was included in the model. Standardized path coefficients were estimated by multiple regression techniques (Asher 1983) and all coefficients not significantly different from zero (t-test, $P_\alpha$=0.05) were set to zero.

In this model, temperature was the strongest factor affecting variation in juvenile brook trout growth rate, having about a 50% greater effect on growth than all ration variables combined. However, indirect effects of temperature acting on growth rate through the ration variables were substantial and accounted for approximately half of the total temperature effect. Ration effects on trout growth rate were also statistically significant, with the predator taxa being slightly more important than filter-feeding primary consumers. Biomass of both groups increased with increasing temperature and together provided the basis for temperature's indirect effect on trout. Path coefficients for the grazers were not significantly different from zero. This was due to the high variances in the grazer biomass data, and is not surprising given the disease induced collapses of the dominant grazer *Glossosoma nigrior* that occurred at several sites during this study (Kohler and Wiley 1997).

### *Predictive Regression Models*

The July temperature fluctuation was the most highly correlated thermal variable with growth of brook trout (r=0.801) and formed the base of our models (Table 12). Approximately 65% of the variation in growth was explained by a simple linear regression model using July temperature fluctuation as the independent variable (Table 13).

Macroinvertebrate variables helped explain additional variation in the growth rate of juvenile brook trout. Total biomass ($R^2$ adj.=0.679), total non-predator biomass ($R^2$ adj.=0.686), or total predator biomass ($R^2$ adj.=0.685) all improved the base model (Table 14). The best two-parameter model of this type used the macroinvertebrate trophic ratio as a measure of the macroinvertebrate community and explained approximately 72% of the variation in brook trout growth (Table 14). Using non-predator macroinvertebrate biomass and macroinvertebrate predator biomass with July temperature fluctuation as separate predictors of growth rate did not greatly improve this model ($R^2$ adj.=0.725) (Table 14).

We developed additional multi-parameter models for predicting growth of juvenile brook trout using stepwise regression. The best fitting model we could achieve included the July temperature fluctuation, standing stocks of *Isogenoides* and filter-feeding macroinvertebrates and the total phosphorus concentration ($R^2$ adj.=0.856) (Table 15).

## Discussion

### *Ration and Trout Growth*

Several studies have observed food limitations (Ensign et al 1990, Cunjak et al 1987, Cunjak and Power 1987) in trout streams. In these studies food consumption was found to restrict growth rates under extreme temperature conditions. Alexander and Gowing (1976) suggested that quantity, not quality, of food was the more important factor in determining growth of trout in Michigan. Waters (1988) reviewed the relationships between fish-production and benthos-production and reaffirmed the "Allen paradox" indicating instream food production is generally insufficient to support observed fish productivity. In this study we have shown that ration availability, as measured by benthic macroinvertebrate standing crop on rock surfaces, is an important and statistically significant predictor of brook trout juvenile growth rate. The relationship between macroinvertebrate biomass (or density) and trout growth is, however, complex and conditioned by temperature and potentially by other controlling variables as well (e.g. water quality).

### *Thermal Habitat and Trout Growth*

Our results indicate that the thermal characteristics of trout streams in the northern Lower Peninsula of Michigan have a strong and pervasive impact on the growth and standing stock of juvenile trout. We found that the mean daily July temperature fluctuation explained 65% of the variation in juvenile brook trout growth rate across our twelve study sites. The correlation between growth and July temperature fluctuation was positive (r=0.80) indicating that sites with higher temperature fluctuations had increased growth rates. Unlike other studies that have observed lower growth rate or condition of salmonids at higher temperatures (Cada et al 1987, Randall and Hawkins 1995) our study was restricted to extremely stable ground water streams (Hinz and Wiley 1997, Wiley et al 1997). In these streams even the highest mean temperatures were well below the optimum growth temperature for brook or brown trout. Meisner (1990) suggested that loss of thermal habitat could occur under various climate change scenarios in Ontario streams leading to negative consequences for trout populations. Our results suggest that small temperature changes in streams with sub-optimal mean temperatures will actually improve juvenile trout growth, particularly if summer maximum temperatures or the magnitude of daily temperature fluctuations are increased.

Water temperature was also found to be positively correlated with macroinvertebrate biomass in this study. Grazer, filter-feeder and total density of non-predaceous macroinvertebrates were all positively correlated with temperature summaries such as maximum and mean daily summer temperature. Invertebrate predator biomass was significantly correlated with July daily temperature flux. Our data suggest that higher standing stocks of macroinvertebrate prey generally occur in waters with higher temperatures. This is a very important result because, as was illustrated in the path analysis, it implies temperature regime affects trout growth by two distinct causal pathways. First, temperature has a direct affect on the physiological rates of trout. In these very cold ground water systems, increases in temperature generally led to significant growth improvement. Beyond this direct effect, increasing temperature also stimulated benthic productivity and thereby increased ration availability and, indirectly, trout growth. Our path analysis suggested that these two effects are roughly equivalent in magnitude given a unit increase in daily temperature flux.

Based on these results we should expect trout populations in small cold Michigan streams to be much more sensitive to changes in thermal regime than physiological studies in the laboratory suggest. Assuming that the physiological effects of warming can be associated with the direct effect of temperature in this analysis, we could expect the growth response to be twice that predicted for the direct effect alone due to increases in ration also driven by temperature. This indirect effect of temperature regime therefore complicates the ecological interpretation of laboratory defined physiological optima. If prey biomass increases with temperature, and that availability can be converted into ration, then the ecologically optimal temperature (or temperature flux) will necessarily be higher than the physiological optimum. Recognizing the potential importance of indirect effects of temperature on fish production and growth could be important in both evaluating trout habitat, and in modeling potential climate effects.

### *Management Applications*

In this study, brook trout YOY growth rate was significantly correlated with both brook trout YOY standing crop, and with the total combined (in these streams: brook, brown, and rainbow trout) biomass of all older (non-YOY) trout (Figure 4). These results suggest that YOY growth may be a useful index of the general trout production potential in smaller colder Michigan streams. The multiple regression equations developed in our study (Tables 13-15) provide a number of relatively simple models for estimating the potential growth rate of juvenile brook trout in small streams of northern Michigan. A simple regression on average July daily temperature flux explained over 65% of the observed variance. More complicated models did better (not surprisingly), but require data on the invertebrate community and/or nutrient concentrations. Two models stand out in terms of potential utility:

$$Y = 0.0352 + 0.01533\,TF + 0.01523\ln(TP)$$

Where $Y$ is juvenile brook trout growth rate; $TF$ is average July daily temperature fluctuation (Celsius); and $TP$ is total phosphorous concentration in ppb (Table 13). Total phosphorus concentrations are often available through Michigan Department of Environmental Quality or can be estimated based on landscape characteristics. The addition of TP increased the explained variance to approximately 71%. If invertebrate community data of the type described in this study are available, the addition of *Isogenoides* and total filter-feeder biomass can increase the $R^2$ to approximately 86% (Table 15).

Juvenile brown trout growth was, in contrast, almost impossible to predict from the data collected in this study. Only 3 of the 12 sites had substantive brown trout populations and brown trout YOY were collected at only 5 sites. There was no evidence that the presence of brown trout had any negative effect on brook trout growth rates. However, YOY brown trout standing stock was negatively related to YOY brook trout standing stock.

A simple causal model of the interrelationships between temperature, YOY growth, YOY standing stocks and adult trout population was parameterized from the data developed in this study (Figure 5). The model suggests that in these small cold streams increases in July temperature will lead to increased juvenile growth of both brook trout and brown trout, as well as increased adult trout standing stocks. For brook trout increases in YOY growth translate into higher year-class strengths (higher YOY standing stocks). However, this did not occur in the case of brown trout (note the path coefficient between $\mathrm{BNT}_{\mathrm{YOY}}$ Biomass and $\mathrm{BNT}_{\mathrm{YOY}}$ growth rate=0). Therefore, the model predicts that despite a strong competitive advantage, increases in brown trout YOY growth will not reduce brook trout standing stocks in these streams. This may indicate that in these cold systems brown trout are so removed from their thermal optimum that small increases in growth performance have little impact on population dynamics. Physical habitat features (e.g. pool availability) or proximity to larger river source populations may be the primary determinants of brown trout standing stocks in these streams.

Both the data and analysis we have presented here suggest that small, ground water dominated brook trout streams may respond to climatic or artificial warming in a way that is quite different from larger and/or warmer trout streams. Despite the fact that brown trout have a higher thermal optimum, and are competitively superior, warming these systems is unlikely to lead to a displacement of brook by brown trout. Furthermore, increases in temperature are likely to increase not decrease growth and standing crop biomass of brook trout as has been anticipated in some warmer Great Lakes area trout streams (Meisner 1990).

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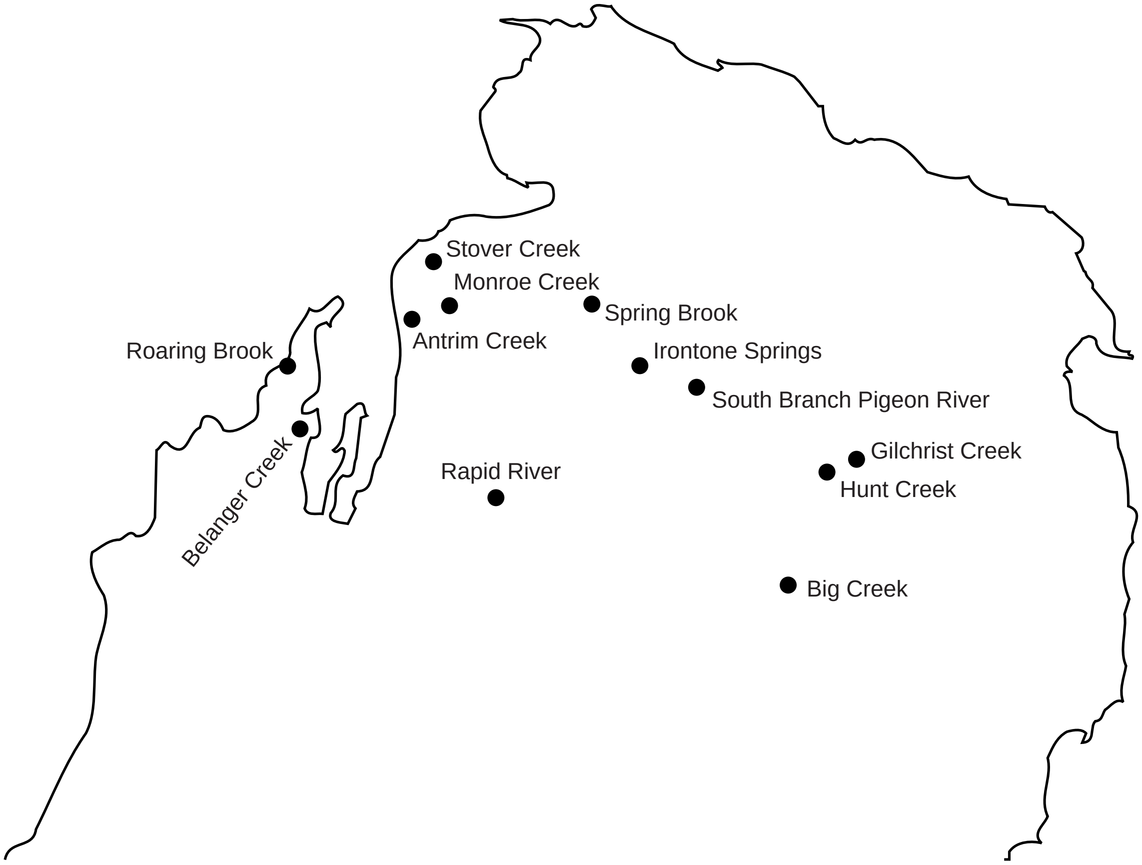


| SITE | T. R. S. | | |
|---|---|---|---|
| Antrim Creek | T. 32 N. | R. 9 W. | S14 |
| Belanger Creek | T. 30 N. | R.11 W. | S10 |
| Big Creek | T. 26 N. | R. 1 E. | S24 |
| Gilchrist Creek | T. 29 N. | R. 3 E. | S27 |
| Hunt Creek | T. 29 N. | R. 2 E. | S35 |
| Irontone Springs | T. 31 N. | R. 3 W. | S15 |
| Monroe Creek | T. 33 N. | R. 7 W. | S31 |
| Rapid River | T. 28 N. | R. 6 W. | S18 |
| Roaring Brook | T. 31 N. | R.11 W. | S 7 |
| Pigeon River | T. 31 N. | R. 2 W. | S35 |
| Spring Brook | T. 33 N. | R. 4 W. | S33 |
| Stover Creek | T. 34 N. | R. 8 W. | S35 |

Figure 1.–Location of sampling sites for study on growth and production of juvenile trout, 1993-95.

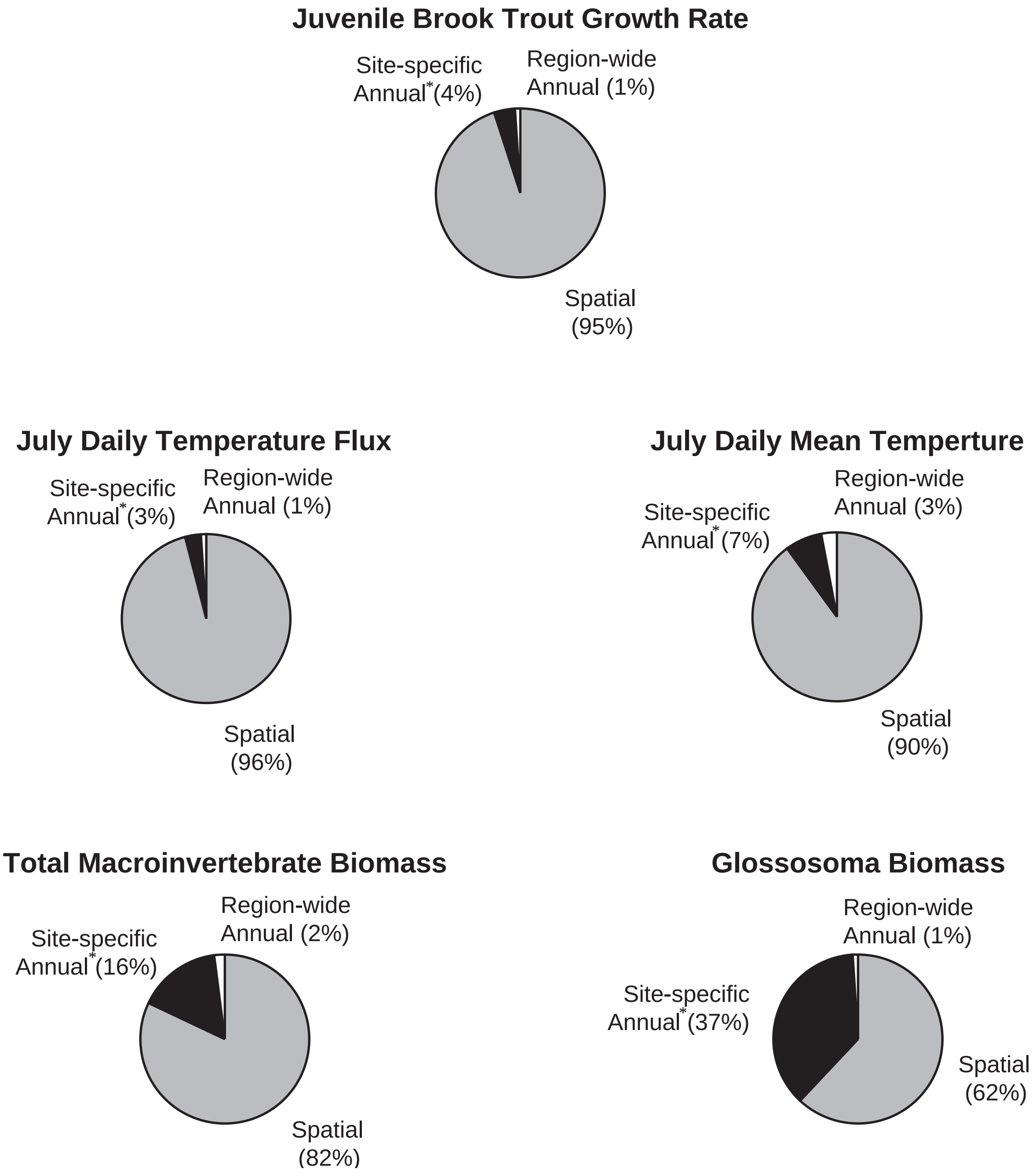
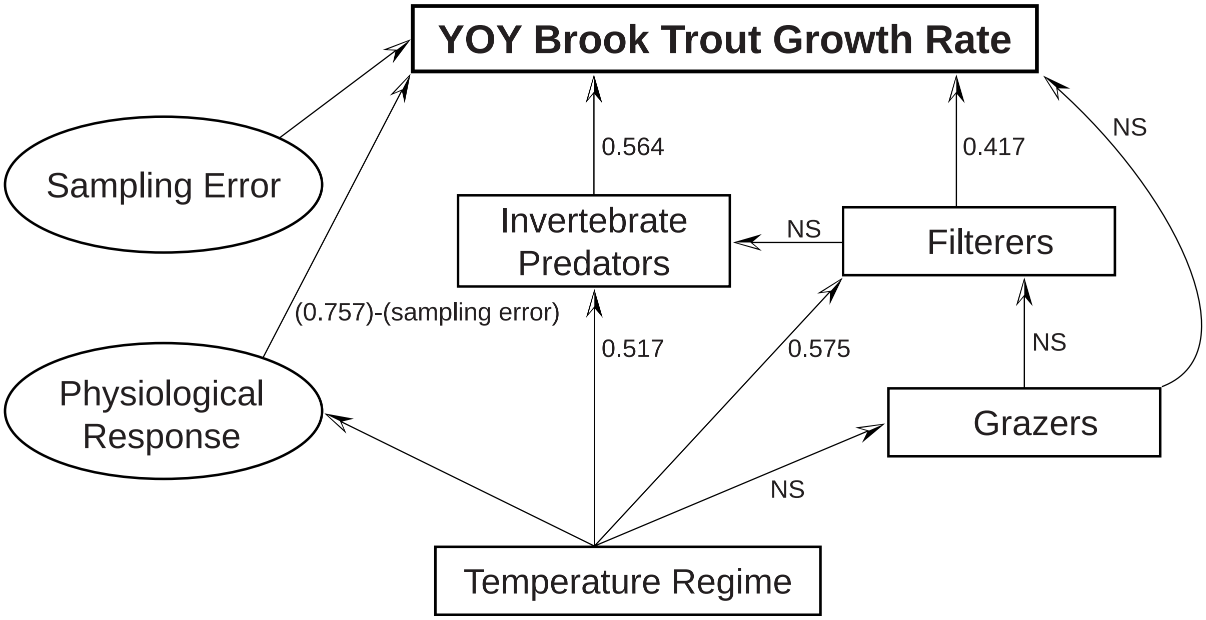


Figure 2.–Variance structure of annual average juvenile brook trout growth rate and key variables from 12 study sites during 1993-95 (n=36). Total variation was partitioned by ANOVA into year, site, and year* site interactions (Wiley et al 1997). Year effect represents regionally coherent (synchronous) annual variation; site effects represent time-averaged spatial variation, and the interaction term represents site-specific annual variation and residual error.



| | Effects on trout growth of: | | | |
|---|---|---|---|---|
| | Invertebrate Predators | Grazers | Filterers | Temperature |
| Pearson correlation | 0.513 | 0.030 | 0.229 | 0.807 |
| Direct effect | 0.564 | NS | 0.417 | 0.757* |
| Indirect effect | none | NS | NS | 0.720 |
| Total effect | 0.564 | NS | 0.417 | 1.477 |

Figure 3.–Path diagram, standardized path coefficients and results of path analysis for a simple model of juvenile brook trout growth. Numbers adjacent to arrows represent the path coefficients in units of standard deviations of the dependent variable per units standard deviation of the independent variable. Temperature = mean daily temperature fluctuation (daily maximum-daily minimum) for the month of July, Invertebrate Predators = LN(mass of *Isogenoides* + mass of *Rhyacophila*), Grazers = LN(mass of all grazing macroinvertebrates), Filterers = LN(mass of all filter-feeding macroinvertebrates). * maximum effect assuming zero sampling error, otherwise = 0.757-sampling error (in standardized units).

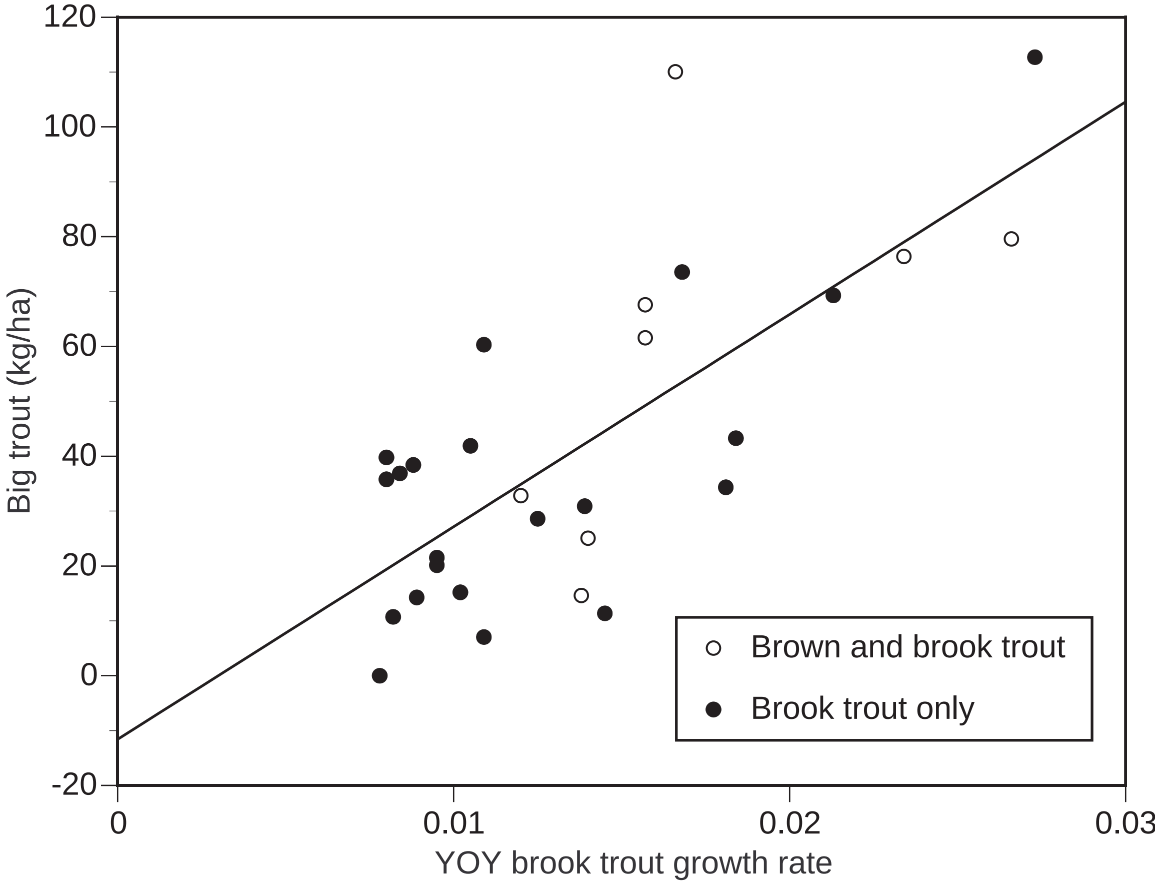


Figure 4.–Relationship between YOY brook trout growth rate (g/day) and standing stock of trout >100 mm total length.

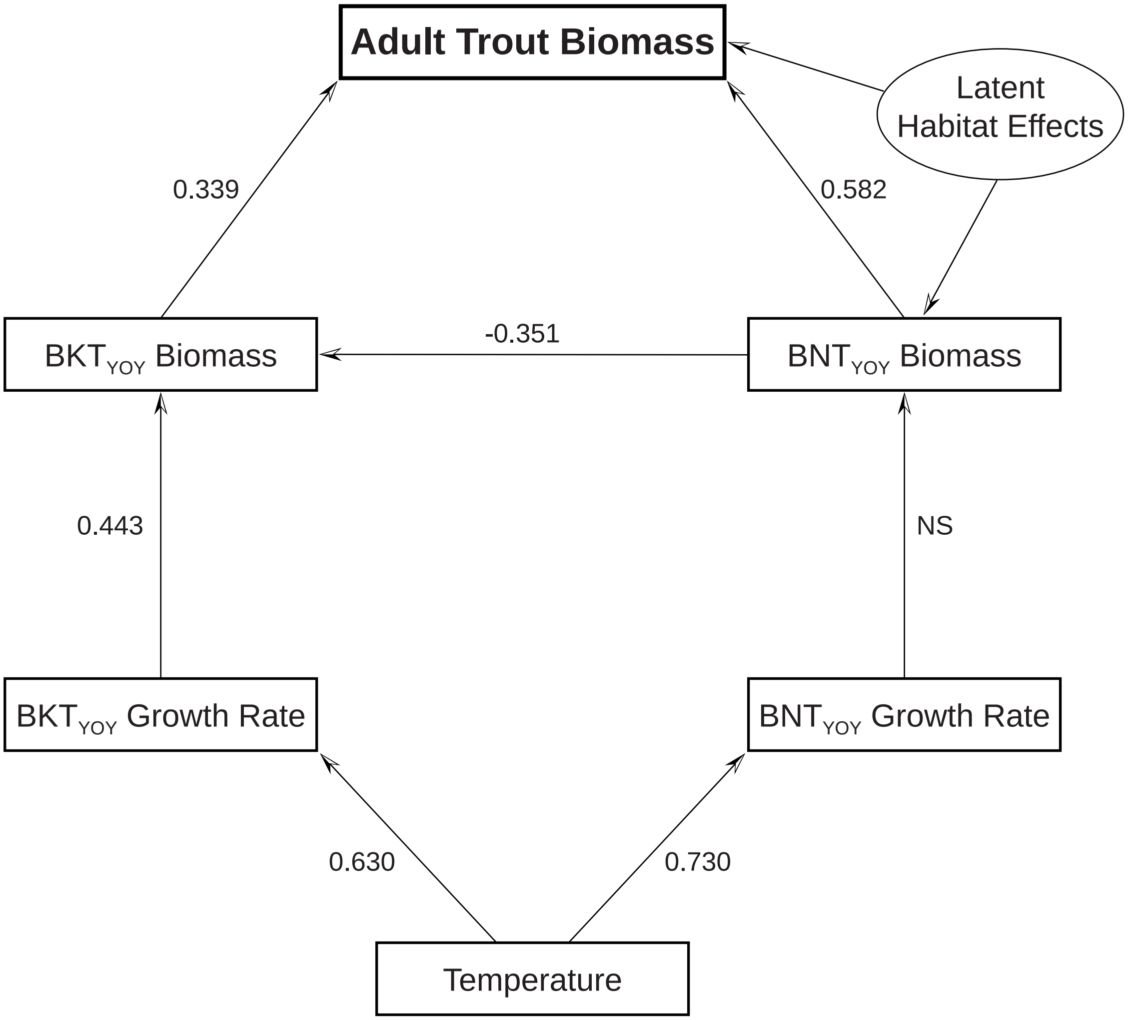


Figure 5.–Path diagram and standardized path coefficients illustrating a simple model of angler-accessible trout production (non-YOY standing stock biomass) based on the data from this study. Numbers adjacent to arrows represent the path coefficients in units of standard deviations of the dependent variable per units standard deviation of the independent variable. Note that ration and physiological effects of temperature on growth are combined, and that indirect effects of temperature on brook trout via brown trout do not occur because of the non-significant path coefficient between brown trout growth and YOY biomass. Temperature = mean daily for the month of July, BKT = brook trout, BNT = brown trout, NS = not statistically significant at $P_a$ -0.05 ( implies a path coefficient of zero). Dashed lines denotes latent habitat effects not modeled but presumed to control brown trout biomass in small coldwater streams.

Table 1.–Selected temperature summaries for 12 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; ATU = accumulated thermal units from January 1 through December 31; Max. = maximum; Min. = minimum; flux = maximum - minimum.

| | Annual | | | Seasonal | | July | | |
|---|---|---|---|---|---|---|---|---|
| Site | Mean ATU | Max.[1] | Min.[1] | Winter mean | Summer mean | Daily mean | Daily flux | N (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 |
| 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 |
| South Branch Pigeon River | 2760 | 22.0 | -1.8 | 2.9 | 12.9 | 16.7 | 3.5 | 3 |
| South Branch Spring Brook | 2652 | 14.0 | 2.0 | 5.8 | 8.7 | 9.5 | 1.2 | 3 |
| Stover Creek | 2753 | 22.1 | -0.5 | 2.0 | 13.0 | 15.8 | 2.8 | 2 |
| Pooled | 2854 | 24.0 | -2.4 | 3.8 | 11.8 | 14.4 | 2.8 | |

[1] Annual maximum and minimum temperatures for period of record.

Table 2.–Average chemical characteristics of study sites based on summer 1996 survey. Phosphorus is reported as P, and all nitrogen parameters as N; TP = total phosphorus; SRP = soluble reactive phosphorus; TN = total nitrogen; NO3-NO2 = nitrate + nitrate nitrogen; NH4 = ammonia nitrogen.

| Site | Alkalinity (mg/l $CaCO_3$) | TP (ppb) | SRP (ppb) | TN (ppb) | $NO_3$-$NO_2$ (ppb) | $NH_4$ (ppb) | pH |
|---|---|---|---|---|---|---|---|
| Antrim Creek | 264 | 13 | 9 | 1,101 | 679 | 21 | 7.7 |
| Belanger Creek | 213 | 40 | 8 | 1,319 | 1,087 | 15 | 7.8 |
| Big Creek | 160 | 11 | 11 | 223 | 59 | 11 | 7.3 |
| Gilchrist Creek | 227 | 16 | 8 | 232 | 47 | 10 | 7.5 |
| Hunt Creek | 211 | 12 | 9 | 186 | 29 | 10 | 7.7 |
| Irontone Springs | 302 | 10 | 16 | 454 | 266 | 15 | 9.0 |
| Monroe Creek | 231 | 17 | 9 | 610 | 290 | 16 | 7.8 |
| Rapid River | 168 | 9 | 7 | 408 | 341 | 8 | 7.6 |
| Roaring Brook | 216 | 17 | 6 | 107 | 1,072 | 8 | 7.6 |
| South Branch Pigeon River | 230 | 8 | 11 | 414 | 128 | 14 | 7.5 |
| South Branch Spring Brook | 205 | 12 | 9 | 261 | 403 | 8 | 7.6 |
| Stover Creek | 255 | 22 | 12 | 1,024 | 595 | 13 | 7.7 |
| Pooled | 224 | 15 | 10 | 609 | 416 | 12 | 7.7 |

Table 3.–Densities of macroinvertebrate feeding guilds and major macroinvertebrate taxa from rock cluster and Hess samples. Mean values for pooled sites and all sampling periods, 1993-95. Some sites were not sampled on all dates due to ice cover.

| | Numerical density (number/$m^2$) | | Standing stock (mg dry mass/$m^2$) | | N |
|---|---|---|---|---|---|
| | Mean | Standard Error | Mean | Standard Error | (samples) |
| **Feeding Guilds** | | | | | |
| Macropredators | 12 | 2 | 142 | 24 | 32 |
| non-predators | 30,651 | 3,459 | 2,244 | 257 | 36 |
| Grazers | 23,907 | 2,447 | 987 | 106 | 36 |
| Filterers | 3,288 | 546 | 931 | 143 | 36 |
| non-Glossosomatid grazing caddis | 3,456 | 1,047 | 326 | 68 | 36 |
| **Major Taxonomic Groups** | | | | | |
| Glossosoma | 1,512 | 436 | 245 | 67 | 36 |
| Protoptila | 3,146 | 1,057 | 212 | 68 | 36 |
| Goera | 26 | 12 | 7 | 4 | 36 |
| Neophylax | 284 | 54 | 108 | 19 | 36 |
| Hydropsychidae | 1,466 | 319 | 479 | 103 | 36 |
| Simuliidae | 1,598 | 488 | 301 | 92 | 36 |
| Brachycentridae | 224 | 62 | 150 | 49 | 36 |
| Chironomidae | 15,750 | 1,743 | 86 | 11 | 36 |
| Baetidae | 2,896 | 413 | 232 | 37 | 36 |
| Ephemerellidae | 293 | 92 | 96 | 34 | 36 |
| Perlidae | 2 | 1 | 21 | 12 | 32 |
| Isogenoides | 3 | 1 | 53 | 12 | 32 |
| Rhyacophila | 5 | 1 | 36 | 10 | 32 |
| **Total** | 32,372 | 3,727 | 2,454 | 289 | 32 |

Table 4.–Standing stock (mg dry mass/m$^2$) of major primary consumer macroinvertebrates from rock samples taken between 1993-95.

| | Hydropsychidae | | Simuliidae | | *Glossosoma* | | Baetidae | |
|---|---|---|---|---|---|---|---|---|
| Site | Mean | Standard Error | Mean | Standard Error | Mean | Standard Error | Mean | Standard Error |
| Antrim Creek | 1,542.5 | 42.5 | 50.2 | 31.3 | 1,091.9 | 309.3 | 125.9 | 3.3 |
| Belanger Creek | 406.3 | 79.7 | 98.0 | 62.6 | 57.2 | 27.9 | 89.2 | 31.9 |
| Big Creek | 160.1 | 61.4 | 967.8 | 431.5 | 118.0 | 92.0 | 233.0 | 75.5 |
| Gilchrist Creek | 202.0 | 58.9 | 721.9 | 536.4 | 109.1 | 68.4 | 120.7 | 54.9 |
| Hunt Creek | 168.9 | 63.8 | 210.6 | 92.0 | 631.9 | 401.6 | 359.0 | 52.2 |
| Irontone Springs | 14.7 | 14.7 | 52.6 | 29.5 | 30.9 | 12.9 | 325.5 | 60.2 |
| Monroe Creek | 774.7 | 131.6 | 104.7 | 96.4 | 50.7 | 39.6 | 24.9 | 10.9 |
| Rapid River | 100.6 | 100.6 | 897.0 | 770.8 | 255.9 | 139.3 | 55.0 | 35.4 |
| Roaring Brook | 13.3 | 6.9 | 200.0 | 64.0 | 134.9 | 133.8 | 604.5 | 68.1 |
| South Branch Pigeon River | 1,746.1 | 460.0 | 201.2 | 78.9 | 433.9 | 227.3 | 194.6 | 80.8 |
| South Branch Spring Brook | 4.9 | 4.9 | 78.5 | 29.5 | 26.9 | 16.9 | 634.4 | 90.4 |
| Stover Creek | 616.1 | 134.1 | 33.6 | 14.9 | 4.1 | 3.2 | 32.2 | 24.3 |
| Pooled | 479.2 | 103.2 | 301.3 | 91.8 | 245.4 | 67.2 | 233.2 | 36.5 |

Table 5.–Standing stock (mg dry mass/m2) of macroinvertebrate predators from supplemental samples taken in February 1993-95. Only one year was sampled for Antrim Creek and Stover Creek due to ice cover. NA = not available; # = also includes all Odonata, Megaloptera, and Atherix, but not predaceous Chironomidae or worms.

| | *Isogenoides* | | *Rhyacophila* | | Perlidae | | all predators# | |
|---|---|---|---|---|---|---|---|---|
| Site | Mean | Standard Error | Mean | Standard Error | Mean | Standard Error | Mean | Standard Error |
| Antrim Creek | 0.0 | NA | 36.5 | NA | 0.8 | NA | 104.7 | NA |
| Belanger Creek | 120.4 | 60.5 | 49.4 | 13.9 | 0.0 | 0.0 | 170.0 | 65.2 |
| Big Creek | 109.9 | 45.0 | 2.9 | 2.6 | 5.0 | 5.0 | 258.2 | 96.8 |
| Gilchrist Creek | 58.6 | 8.5 | 0.0 | 0.0 | 8.5 | 4.1 | 95.6 | 14.0 |
| Hunt Creek | 116.7 | 36.9 | 71.5 | 41.3 | 0.0 | 0.0 | 271.6 | 44.7 |
| Irontone Springs | 7.3 | 7.3 | 7.3 | 4.2 | 0.0 | 0.0 | 27.2 | 11.0 |
| Monroe Creek | 0.0 | 0.0 | 20.4 | 4.4 | 211.5 | 52.0 | 336.4 | 90.8 |
| Rapid River | 9.8 | 4.9 | 12.7 | 5.3 | 0.0 | 0.0 | 26.5 | 8.3 |
| Roaring Brook | 0.0 | 0.0 | 3.4 | 0.6 | 0.0 | 0.0 | 3.4 | 0.6 |
| South Branch Pigeon River | 33.5 | 17.9 | 7.4 | 1.5 | 2.9 | 1.6 | 72.4 | 17.0 |
| South Branch Spring Brook | 112.1 | 28.7 | 95.4 | 42.5 | 0.0 | 0.0 | 207.5 | 50.3 |
| Stover Creek | 0.0 | NA | 0.0 | NA | 0.2 | NA | 29.5 | NA |
| Pooled | 53.3 | 11.5 | 35.5 | 9.7 | 21.4 | 11.7 | 141.9 | 23.6 |

Table 6.–Pearson product-moment correlations between macroinvertebrate summary and thermal parameters. Flux = daily maximum - daily minimum. Bold values indicates significant at P ≤0.05(*) or P ≤0.01(**).

| Parameter | Total Predators | Non-Predators | | | Total Macroinvertebrate |
|---|---|---|---|---|---|
| | | Grazers | Filterers | Pooled | |
| **Thermal Variable** | | | | | |
| **Annual** | | | | | |
| Mean | 0.106 | 0.217 | 0.133 | 0.246 | 0.233 |
| Maximum | 0.195 | 0.294 | **0.469**$^{**}$ | **0.509**$^{**}$ | **0.564**$^{**}$ |
| Flux | 0.234 | 0.281 | **0.352**$^{*}$ | **0.381**$^{*}$ | **0.390**$^{*}$ |
| **Winter** | | | | | |
| Mean | -0.181 | 0.101 | -0.282 | 0.042 | -0.114 |
| Maximum | 0.241 | 0.060 | -0.063 | -0.069 | 0.073 |
| Flux | -0.085 | -0.006 | 0.023 | 0.015 | -0.028 |
| **Summer** | | | | | |
| Mean | 0.299 | 0.159 | **0.526**$^{**}$ | **0.414**$^{*}$ | **0.499**$^{**}$ |
| Maximum | 0.144 | 0.334 | **0.412**$^{*}$ | **0.503**$^{**}$ | **0.534**$^{**}$ |
| Flux | **0.378**$^{*}$ | **0.391**$^{*}$ | **0.482**$^{**}$ | **0.522**$^{**}$ | **0.554**$^{**}$ |
| **July** | | | | | |
| Mean | 0.210 | 0.188 | **0.545**$^{**}$ | **0.474**$^{**}$ | **0.535**$^{**}$ |
| Maximum | 0.163 | 0.299 | **0.391**$^{*}$ | **0.459**$^{**}$ | **0.497**$^{**}$ |
| Flux | 0.294 | **0.371**$^{*}$ | **0.439**$^{*}$ | **0.481**$^{**}$ | **0.509**$^{**}$ |
| **Macroinvertebrate Variable** | | | | | |
| Total macroinvertebrate | 0.265 | **0.809**$^{**}$ | **0.825**$^{**}$ | **0.997**$^{**}$ | **1.000**$^{**}$ |
| Total Predators | **1.000**$^{**}$ | 0.289 | 0.014 | 0.186 | 0.265 |
| Non-Predators | | | | | |
| Grazers | 0.289 | **1.000**$^{**}$ | **0.386**$^{*}$ | **0.809**$^{**}$ | **0.829**$^{**}$ |
| Filterers | 0.014 | **0.386**$^{*}$ | **1.000**$^{**}$ | **0.826**$^{**}$ | **0.825**$^{**}$ |
| Pooled | 0.186 | **0.809**$^{**}$ | **0.826**$^{**}$ | **1.000**$^{**}$ | **0.997**$^{**}$ |

Table 7.–Juvenile (YOY) brook trout densities at study sites as mean values for all sampling periods, 1993-95. SD = standard deviation.

| Site | Numerical density (number/ha) Mean | Numerical density (number/ha) SD | Standing stock (kg/ha) Mean | Standing stock (kg/ha) SD | 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 |
| Gilchrist Creek | 105 | NA | 0.96 | NA | 1 |
| Hunt Creek | 4,598 | 2,141 | 27.70 | 9.34 | 3 |
| Irontone Springs | 1,162 | 981 | 4.66 | 4.68 | 3 |
| Monroe Creek | 903 | 180 | 4.16 | 0.48 | 3 |
| Rapid River | 5,776 | 309 | 23.84 | 2.78 | 3 |
| Roaring Brook | 2,269 | 624 | 7.30 | 2.15 | 3 |
| South Branch Pigeon River | 1,669 | 776 | 10.29 | 4.34 | 3 |
| South Branch Spring Brook | 1,199 | 209 | 3.98 | 0.44 | 3 |
| Stover Creek | 924 | NA | 4.71 | NA | 1 |
| Pooled | 1,822 | 1,946 | 8.39 | 9.65 | NA |

Table 8.–Juvenile (YOY) brook trout size and growth rate at study sites as mean values for all sampling periods, 1993-95. Hunt Creek was sampled approximately 70 days earlier than the other sites. NA = not available. # = No juvenile brook trout were captured from this site in one of these years. SD = standard deviation.

| Site | Size (g wet weight) Mean | Size (g wet weight) SD | Growth Rate (g/day) Mean | Growth Rate (g/day) SD | N (years) |
|---|---|---|---|---|---|
| Antrim Creek | 2.9 | 0.3 | 0.0084 | 0.0009 | 3 |
| Belanger Creek | 5.7 | 0.2 | 0.0162 | 0.0006 | 3 |
| Big Creek | 5.6 | NA | 0.0157 | NA | 2# |
| Gilchrist Creek | 9.1 | NA | 0.0266 | NA | 1 |
| Hunt Creek | 6.3 | 0.9 | 0.0240 | 0.0030 | 3 |
| Irontone Springs | 3.7 | 0.8 | 0.0105 | 0.0022 | 3 |
| Monroe Creek | 4.6 | 0.4 | 0.0133 | 0.0011 | 3 |
| Rapid River | 4.2 | 0.7 | 0.0118 | 0.0019 | 3 |
| Roaring Brook | 3.0 | 0.2 | 0.0084 | 0.0004 | 3 |
| South Branch Pigeon River | 6.3 | 0.3 | 0.0178 | 0.0009 | 3 |
| South Branch Spring Brook | 3.3 | 0.3 | 0.0095 | 0.0007 | 3 |
| Stover Creek | 5.1 | NA | 0.0145 | NA | 1 |
| Pooled | 4.6 | 1.6 | 0.0138 | 0.0055 | NA |

Table 9.–Juvenile (YOY) brown trout densities at study sites as mean values for all sampling periods, 1993-95. SD = standard deviation.

| Site | Numerical density (number/ha) |  | Standing stock (kg/ha) |  | N (years) |
|---|---|---|---|---|---|
|  | Mean | SD | Mean | SD |  |
| Antrim Creek | 0 | 0 | 0.00 | 0.00 | 3 |
| Belanger Creek | 3,307 | 1,491 | 18.91 | 7.46 | 3 |
| Big Creek | 2,247 | 555 | 12.79 | 4.78 | 2 |
| 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 |
| South Branch Pigeon River | 0 | 0 | 0.00 | 0.00 | 3 |
| South Branch Spring Brook | 0 | 0 | 0.00 | 0.00 | 3 |
| Stover Creek | 0 | NA | 0.00 | NA | 1 |
| Pooled | 539 | 1170 | 3.14 | 6.67 | NA |

Table 10.–Juvenile (YOY) brown trout size and growth rate at study sites as mean values for all sampling periods, 1993-95. Hunt Creek was sampled approximately 70 days earlier than the other sites. NA = not available. NC = none captured. # = no juvenile brown trout were captured from this site in only two of these years. SD = standard deviation.

| | Size (g wet weight) | | Growth Rate (g/day) | | N |
|---|---|---|---|---|---|
| Site | Mean | SD | Mean | SD | (years) |
| Antrim Creek | NC | NC | NC | NC | 3 |
| Belanger Creek | 5.9 | 1.0 | 0.0167 | 0.0029 | 3 |
| Big Creek | 5.6 | 0.7 | 0.0158 | 0.0022 | 2 |
| Gilchrist Creek | 7.5 | NA | 0.0218 | NA | 1 |
| Hunt Creek | 5.1 | NA | 0.0195 | NA | 3# |
| Irontone Springs | NC | NC | NC | NC | 3 |
| Monroe Creek | 5.6 | 1.0 | 0.0158 | 0.0028 | 3 |
| Rapid River | NC | NC | NC | NC | 3 |
| Roaring Brook | NC | NC | NC | NC | 3 |
| South Branch Pigeon River | NC | NC | NC | NC | 3 |
| South Branch Spring Brook | NC | NC | NC | NC | 3 |
| Stover Creek | NC | NC | NC | NC | 1 |
| Pooled | 5.8 | 1.0 | 0.0170 | 0.0029 | NA |

Table 11.–Pearson product-moment correlations between juvenile trout population characteristics and macroinvertebrate standing stocks (mg dry mass/m2) from 12 sites sampled during 1993-95. Bold values indicates significant at P≤0.05(*) or P≤0.01(**). All degrees of freedom for brook trout are 27. Brown trout standing stock has 29 and brown trout growth has 8 degrees of freedom. GR = Growth rate; SS = Standing Stock; Trophic Ratio = mass of Macro-Preds/mass of Non-Preds; other Caddis = all non-Glossosomatidae grazing Trichoptera.

| | Brook Trout | | | Brown Trout |
|---|---|---|---|---|
| Summary parameter | Growth rate (g/day) | Standing stock (Kg/ha) | Growth rate (g/day) | Standing stock (Kg/ha) |
| **Trout variables** | | | | |
| GR brook | **1.000**$^{**}$ | **0.381**$^{*}$ | **0.723**$^{*}$ | 0.177 |
| SS brook | **0.381**$^{*}$ | **1.000**$^{**}$ | 0.263 | -0.343 |
| GR brown | **0.723**$^{**}$ | 0.263 | **1.000**$^{**}$ | -0.094 |
| SS brown | 0.177 | -0.343 | -0.094 | **1.000**$^{**}$ |
| **Macroinvertebrate Variables** | | | | |
| Trophic Ratio | 0.255 | 0.003 | -0.057 | **0.410**$^{**}$ |
| Non-Predators | 0.162 | -0.107 | -0.451 | -0.037 |
| Filterers | 0.090 | -0.010 | -0.431 | -0.004 |
| Hydropsychidae | 0.037 | -0.174 | -0.409 | -0.092 |
| Simuliidae | -0.073 | 0.223 | 0.043 | 0.106 |
| Grazers | 0.157 | -0.094 | -0.406 | -0.134 |
| Baetidae | -0.264 | 0.034 | 0.331 | -0.281 |
| *Glossosoma* | 0.119 | 0.152 | -0.360 | -0.232 |
| other Caddis | 0.181 | -0.243 | -0.467 | 0.062 |
| Chironomidae | -0.054 | 0.241 | -0.519 | -0.111 |
| Macro-Predators | 0.302 | -0.018 | -0.117 | 0.276 |
| Perlidae | -0.055 | -0.157 | -0.103 | 0.070 |
| *Isogenoides* | 0.354 | 0.051 | -0.031 | **0.435**$^{*}$ |
| *Rhyacophila* | **0.400**$^{*}$ | 0.319 | 0.045 | -0.087 |
| **Total** | 0.214 | -0.097 | -0.459 | -0.007 |

Table 12.–Pearson product-moment correlations between juvenile trout population characteristics and thermal or chemical parameters from 12 sites sampled for temperature and trout in 1993-95. Bold values indicates significant at P ≤0.05(*) or P ≤0.01(**). Brook trout degrees of freedom are 32, brown trout growth has 8, and brown trout density and standing stock have 32. Not all sites were sampled each year, and chemistry data are summaries from 1996. Winter period is from November 1 through April 30; summer period is from May 1 through October 30; Flux = daily maximum - daily minimum; TP = total phosphorus; SRP = soluble reactive phoshorus; TIN = total inorganic nitrogen.

|  | Brook Trout |  |  | Brown Trout |  |  |
|---|---|---|---|---|---|---|
| Summary parameter | Growth (g/day) | Density (number/ha) | Standing stock (kg/ha) | Growth (g/day) | Density (number/ha) | Standing stock (kg/ha) |
| **Thermal Variables** |  |  |  |  |  |  |
| **Annual** |  |  |  |  |  |  |
| Mean | 0.204 | -0.304 | -0.233 | -0.236 | 0.206 | 0.229 |
| Maximum | **0.437**$^{*}$ | **-0.365**$^{*}$ | -0.211 | -0.151 | 0.251 | 0.270 |
| Flux | **0.800**$^{**}$ | 0.272 | **0.436**$^{*}$ | 0.358 | 0.138 | 0.150 |
| **Winter** |  |  |  |  |  |  |
| Mean | 0.093 | 0.024 | -0.003 | -0.119 | -0.019 | -0.003 |
| Maximum | 0.243 | -0.140 | -0.064 | -0.170 | **0.403**$^{*}$ | **0.440**$^{*}$ |
| Flux | **0.364**$^{*}$ | 0.284 | 0.303 | 0.461 | 0.142 | 0.158 |
| **Summer** |  |  |  |  |  |  |
| Mean | 0.129 | **-0.360**$^{*}$ | -0.235 | -0.313 | 0.195 | 0.198 |
| Maximum | **0.374**$^{*}$ | **-0.389**$^{*}$ | -0.246 | -0.266 | 0.235 | 0.247 |
| Flux | **0.786**$^{**}$ | 0.148 | **0.357**$^{*}$ | 0.220 | 0.088 | 0.094 |
| **July** |  |  |  |  |  |  |
| Mean | **0.401**$^{*}$ | **-0.408**$^{*}$ | -0.257 | 0.239 | 0.291 | 0.316 |
| Maximum | **0.403**$^{*}$ | -0.333 | **0.460**$^{**}$ | -0.076 | 0.250 | 0.259 |
| Flux | **0.801**$^{**}$ | 0.270 | -0.188 | 0.261 | 0.024 | 0.025 |
| **Chemical variables** |  |  |  |  |  |  |
| Alkalinity | -0.197 | **-0.376**$^{*}$ | -0.287 | 0.183 | -0.276 | -0.275 |
| TP | 0.298 | **-0.352**$^{*}$ | -0.269 | -0.077 | **0.749**$^{**}$ | **0.754**$^{**}$ |
| SRP | -0.004 | -0.346 | -0.247 | -0.408 | -0.083 | -0.087 |
| TIN | **-0.432**$^{*}$ | -0.331 | **-0.416**$^{*}$ | -0.210 | **0.355**$^{*}$ | **0.353**$^{*}$ |
| $NO_3$-$NO_2$ | **-0.546**$^{**}$ | -0.210 | **-0.354**$^{*}$ | -0.171 | 0.326 | 0.321 |
| $NH_4$ | -0.137 | **-0.495**$^{**}$ | **-0.415**$^{*}$ | -0.398 | 0.098 | 0.100 |
| pH | -0.253 | -0.102 | -0.120 | -0.078 | -0.138 | -0.140 |

Table 13.–Results of linear regressions of growth rate (g/day) of juvenile trout with simple water temperature summaries and total phosphorus. Bolded F-statistics and variables are statistically significant for the model. F = F-statistic; July flux = mean of daily maximum - daily minimum temperatures for the month of July; TP = total phosphorus; SR = square root transformation; ln = natural logarithm transformation.

| Dependent variable | Independent variable | Coefficient | P | F | P | df | $R^2$ |
|---|---|---|---|---|---|---|---|
| Brook trout growth (SR) | **July flux** | 0.016517 | ≤0.0001 | **50.4** | ≤0.001 | 27 | 0.651 |
| | **constant** | 0.070807 | ≤0.0001 | | | | |
| Brown trout growth (SR) | July mean | 0.098552 | 0.0727 | 0.4 | >0.500 | 8 | 0.052 |
| | constant | 0.000198 | 0.5267 | | | | |
| Brook trout growth (SR) | **July flux** | 0.015330 | ≤0.0001 | **34.6** | <0.001 | 2, 26 | 0.706 |
| | **TP (ln)** | 0.015228 | 0.0126 | | | | |
| | **constant** | 0.035231 | 0.0232 | | | | |

Table 14.–Results of multiple linear regressions of growth rate (g/day) of juvenile trout with simple water temperature and macroinvertebrate summaries. Bolded F-statistics and variables are statistically significant for the model. F = F-statistic; July flux = mean of daily maximum - daily minimum temperatures for the month of July; Total Macros = total macroinvertebrate biomass; Non-Preds = total non-predator macroinvertebrate biomass; Macro-Preds = total macroinvertebrate predator biomass; Trophic ratio is the macroinvertebrate predator biomass/macroinvertebrate non-predator biomass; SR = square root transformation; ln = natural logarithm transformation.

| Dependent variable | Independent variable | Coefficient | P | F | P | df | $R^2$ adjusted |
|---|---|---|---|---|---|---|---|
| Brook trout growth (SR) | **July flux** | 0.017865 | ≤0.0001 | **28.6** | <0.001 | 2, 24 | 0.679 |
| | Total Macros (ln) | -0.007311 | 0.1229 | | | | |
| | **constant** | 0.123860 | 0.0007 | | | | |
| Brook trout growth (SR) | **July flux** | 0.018888 | ≤0.0001 | **31.7** | <0.001 | 2, 26 | 0.686 |
| | **Non-Preds (ln)** | -0.009707 | 0.0315 | | | | |
| | **constant** | 0.137412 | 0.0001 | | | | |
| Brook trout growth (SR) | **July flux** | 0.014441 | ≤0.0001 | **29.3** | <0.001 | 2, 24 | 0.685 |
| | Macro-Preds (ln) | 0.003076 | 0.0939 | | | | |
| | **constant** | 0.065226 | ≤0.0001 | | | | |
| Brook trout growth (SR) | **July flux** | 0.015018 | ≤0.0001 | **34.3** | <0.001 | 2, 24 | 0.719 |
| | **Trophic Ratio (ln)** | 0.003979 | 0.0191 | | | | |
| | **constant** | 0.089755 | ≤0.0001 | | | | |
| Brook trout growth (SR) | **July flux** | 0.016504 | ≤0.0001 | **23.8** | <0.001 | 3, 23 | 0.725 |
| | **Non-Preds (ln)** | -0.008528 | 0.0460 | | | | |
| | Macro-Preds (ln) | 0.003381 | 0.0553 | | | | |
| | **constant** | 0.122430 | 0.0002 | | | | |

Table 15.–Results of stepwise regression for growth rate (g/day) of juvenile brook trout with simple water temperature, water chemistry, and macroinvertebrate summaries. Bolded F-statistics and variables are statistically significant for the model ($\alpha$=0.05). F = F-statistic; July flux = mean of daily maximum - daily minimum temperatures for the month of July; Isogenoides = dry mass of Isogenoides/m$^2$; TP = total phosphorus as P; Filterers = dry mass of all filter-feeding macroinvertebrates except chironomids and molluscs; SR = square root transformation; ln = natural logarithm transformation.

| Dependent variable | Independent variable | Coefficient | P | F | P | df | $R^2$ adjusted |
|---|---|---|---|---|---|---|---|
| Brook trout growth (SR) | **July flux** | 0.015228 | ≤0.0001 | **39.6** | <0.001 | 4, 22 | 0.856 |
| | **Isogenoides (SR)** | 0.001125 | 0.0052 | | | | |
| | **1/(TP (SR))** | -0.159553 | 0.0001 | | | | |
| | **Filterers (ln)** | -0.003577 | 0.0280 | | | | |
| | **constant** | 0.137470 | ≤0.0001 | | | | |

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