

Population regulation of brook trout (*Salvelinus fontinalis*) in Hunt Creek, Michigan: a 50-year study

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SUMMARY

1. Fisheries models generally are based on the concept that strong density dependence exists in fish populations. Nonetheless, there are few examples of long-term density dependence in fish populations.
2. Using an information theoretical approach (AIC) with regression analyses, we examined the explanatory power of density dependence, flow and water temperature on the *per capita* rate of change and growth (annual mean total length) for the whole population, adults, 1+ and young-of-the-year (YOY) brook trout (*Salvelinus fontinalis*) in Hunt Creek, Michigan, USA, between 1951 and 2001. This time series represents one of the longest quantitative population data sets for fishes.
3. Our analysis included four data sets: (i) Pooled (1951–2001), (ii) Fished (1951–65), (iii) Unfished (1966–2001) and (iv) Temperature (1982–2001).
4. Principle component analyses of winter flow data identified a gradient between years with high mean daily winter flows, high daily maximum and minimum flows and frequent high flow events, and years with an opposite set of flow characteristics. Flows were lower during the Fished Period than during the Unfished Period. Winter temperature analyses elucidated a gradient between warm mean, warm minimum and maximum daily stream temperatures and a high number of minimum daily temperatures >6.1 °C, and years with the opposite characteristics. Summer temperature analyses contrasted years with warm summer stream temperatures vs years with cool summer stream temperatures.
5. Both YOY and adult densities varied several-fold during the study. Regression analysis did not detect a significant linear or nonlinear stock–recruitment relationship. AIC analysis indicated that density dependence was present in 15 of 16 cases (four population segments × four data sets) for both *per capita* rate of increase (w_i values 0.46–1.00) and growth data (w_i values 0.28–0.99). The almost ubiquitous presence of density dependence in both population and growth data is concordant with results from other trout populations and other studies in Michigan.

Keywords: density dependence, density independence, exploitation, population dynamics, trout fishing

Introduction

The concept of density dependence has been a foundation of biology since at least the time of Thomas Malthus. Briefly stated, density dependence means that populations will respond in a compensatory manner to changes in abundance; consequently, when abundance is low, the *per capita* rate of increase will be high and *vice versa*.

Density dependence may be manifested in any aspect of demography including population abundance, individual growth rates, individual reproductive rates or mortality. Density dependence is a theoretical cornerstone of both ecology and biological resource management, where some form of density dependence typically is found in virtually all models involving population or community dynamics or harvesting. Despite the importance of this concept, its

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documentation, especially over ecologically significant time periods, has been less frequent than might be expected (Grossman *et al.*, 2006; Johnston *et al.*, 2007). There are a variety of reasons for this shortcoming including sampling constraints and imprecision, statistical difficulties in detection and environmental change that limits sample comparability (Grossman *et al.*, 2006). These effects have been described in detail elsewhere but all primarily involve the difficulties of obtaining accurate long-term time series of data where the effects of natural and anthropogenic processes can be disentangled (Grossman *et al.*, 2006; Johnston *et al.*, 2007).

The difficulty of quantifying the importance and strength of density dependence in exploited populations is particularly acute, because we rarely have demographic time series for exploited species prior to the onset of exploitation. In these populations, density dependence is most commonly identified when exploitation drives populations to levels that are sufficiently low that positive linear or curvilinear responses are detected between abundance and recruitment (i.e. ascending limbs of stock–recruitment curves such as Ricker or Beverton–Holt curves; Elliott & Elliott, 2006). When this occurs, the population already has been driven to low levels and may be strongly subject to the unpredictable effects of environmental variation such as unusual shifts in currents or temperature or floods or droughts. Attempting to assess the strength of density dependence within exploited populations when they have been driven to low levels is a risky approach. Given that successful management of any exploited population is dependent on the ability of these populations to respond to harvesting in a density-dependent manner (i.e. via compensatory reproduction, growth or survivorship), it is obvious that there is great need for estimates of the effects of density dependence on natural populations, especially those that have been exploited or are likely to undergo exploitation.

Salmonid fishes are excellent test organisms for multiple aspects of ecological theory because they display strong behavioural- and population-level interactions on both an intra- and interspecific basis (Elliott, 1994; Peterson & Fausch, 2003) and also are economically important (Grossman *et al.*, 2010). Density dependence has been observed in a number of salmonid species including members of the genera *Oncorhynchus*, *Salmo* and *Salvelinus* (Elliott & Hurley, 1998; Grant & Imre, 2005; Lobon-Cervia, 2007a,b; Zorn & Nuhfer, 2007a), but density-independent factors also affect population processes in this group (Fausch *et al.*, 2001; Hakala & Hartman, 2004; Zorn & Nuhfer, 2007b; Lobon-

Cervia, 2009). Salmonids typically exhibit intraspecific competition via behavioural interactions for food or space or a combination of the two resources (Grossman *et al.*, 2010), but most investigations have not directly linked competition to population-level processes (e.g. what is quantified are niche shifts or differences in growth, but not changes in abundance or density, but see Zorn & Nuhfer, 2007a).

In this study, we test for the relative importance of density-dependent and density-independent forces, as well as recruitment limitation, on the *per capita* rate of increase and growth of various population segments of a population of brook trout (*Salvelinus fontinalis* Mitchell) resident in Hunt Creek, Michigan. Brook trout are the only salmonid native to inland waters in eastern North America, and many populations are showing declines (Hudy *et al.*, 2008). Our study population at the Hunt Creek Fisheries Research Station of the Michigan Department of Natural Resources has been sampled quantitatively since 1949 (Alexander & Nuhfer, 1993). This population was subject to fishing with a ten fish per day limit and minimum size for harvesting of 178 mm, between 1950 and 1965 (Alexander & Nuhfer, 1993), but was free from exploitation between 1966 and 2001. Consequently, it is possible to quantify the relative importance of the potential regulatory processes in both the presence and absence of exploitation. This time series constitutes one of the longest quantitative population records for a vertebrate.

Methods

Study site

Hunt Creek is located in north-eastern portion of Michigan's Lower Peninsula and is a groundwater-fed stream draining highly permeable glacial deposits of gravels and sands. The creek has stable flows (Nuhfer & Baker, 2004) and is typical of relatively undisturbed streams in the region. Our analyses are based on a 50-year time series of population estimates for brook trout collected in Section C of Hunt Creek, which is 1254 m in length and 0.48 ha at summer base flows. The study site (in some publications termed RZ) is described extensively in the studies by Alexander & Nuhfer (1993), Nuhfer (2004) and Nuhfer & Baker (2004). The only other species regularly found in this section of the creek are the sculpins *Cottus cognatus* Richardson and *C. bairdi* Girard, although a few transient species of minnows, darters and sticklebacks also occasionally were captured (Alexander & Nuhfer, 1993).

Environmental data

Flow. Daily flow measurement ($\text{m}^3 \text{s}^{-1}$) data were available for Hunt Creek from 1998 to 2009 via a stream gauge located just below the study section. These data include daily mean, maximum and minimum flows ($\text{m}^3 \text{s}^{-1}$); however, the time series lacked data for 1–31 January and 1 October to 31 December 1998, 1 January to 20 March 1999, 19 September to 21 October 2002, 10 to 18 October 2005, 30 July to 9 September 2007, 14 July to 31 December 2008, 1 January to 29 March and 7 September to 3 November 2009. Because this time series only covered a portion of the trout data set, we correlated mean daily flows from Hunt Creek with mean daily flow data ($\text{m}^3 \text{s}^{-1}$) from the nearby Pigeon River (USGS Water Data website, gauge 04128990). Maximum and minimum daily flows were not available from this gauge. Flow data for the Pigeon River were available from 1 November 1950 through 31 December 2009 without any gaps. The correlation analysis was based on the period of overlap (1998–2009) and then used to retrodict flows in Hunt Creek between 1951 and 1999. We were interested in the effects of winter flows on growth and survivorship of brook trout, so we based the correlation analysis on daily flows between 1 November and 31 March. The correlation analysis yielded the following regression equation $y = 0.0894x + 17.432$ with an R^2 of 0.57.

We then calculated a variety of annual flow values for the period 1 November to 31 March including (i) mean annual daily flow, (ii) minimum annual daily flow, (iii) annual maximum daily flow, (iv) annual number of days with high flows and (v) annual number of days with low flows. High and low flows represented the highest and lowest 10% of mean daily flows, respectively, and were $>0.74 \text{ m}^3 \text{ s}^{-1}$ (high) and $<0.65 \text{ m}^3 \text{ s}^{-1}$ (low). We log-transformed these five flow variables (variable + 1) and then used them in a principle component analysis (PCA) using a correlation matrix solution. The first component explained 63% of the variance in the data, and annual scores on this component were used in subsequent analyses as a representation of the effects of density-independent forces.

Temperature. Daily water temperatures were available from 3 October 1992 through 30 November 2009. Submerged electronic thermometers were located near the upstream and downstream boundaries of the study site and recorded water temperatures hourly (Nuhfer & Baker, 2004). We used the mean of these two measures to calculate (i) mean daily water temperature, (ii) maximum daily water temperature and (iii) minimum daily water temperature.

Because we did not have water temperature data for the entire time series, we correlated water temperature data from Hunt Creek with air temperatures from the nearby Gaylord weather station (National Weather Service) to retrodict water temperatures between 1982 and 1991; unfortunately, data prior to 1982 were not available from this station. Regressions for daily mean, maximum and minimum water temperatures all had R^2 values > 0.90 (mean daily water temperature: $y = 0.0044x^2 + 0.3157x + 5.1389$ with $R^2 = 0.93$, maximum daily water temperature: $y = 0.004x^2 + 0.2816x + 4.7463$ with $R^2 = 0.92$, minimum daily water temperature: $y = 0.0045x^2 + 0.3568x + 5.968$, $R^2 = 0.90$). The Gaylord station was missing temperature data from winter 1984 through most of 1985, so these dates were not used in analyses.

Given that winter and summer temperatures affect fish differently, we created separate data sets for these seasons. The winter temperature data set consisted of seven temperature variables collected between 1 November and 31 March: (i) mean daily water temperature, (ii) mean minimum daily water temperature, (iii) mean maximum daily water temperature, (iv) lowest mean daily water temperature, (v) highest mean daily water temperature, (vi) number of days with low water temperature and (vii) number of days with high water temperature. As with flow categories, low and high water temperatures were defined as any temperature within the lowest and highest 10% of all temperatures, with the respective threshold values being 1.83 and 6.06 °C, respectively. The lowest winter temperature was slightly <0 for 1984 and was rounded up to zero. Analyses of summer water temperature data included the same seven temperature measurements for the 1 June–31 August period. For summer data, low and high temperature thresholds were 10.7 and 15.0 °C, respectively, which represented the lowest and highest 10% of all measurements. We used PCA with a correlation matrix solution, to analyse temperature data sets. The counts of low and high temperatures were similar to counts for flows and had 0 values, so we transformed those variables using $\log(\text{variable} + 1)$. The transformation improved the normality for three of the four variables. There was little evidence of non-normality in temperature data with the exception of the number of high and low temperature days, so only these variables were transformed using $\log(\text{variable} + 1)$. PCA is generally robust with respect to minor deviations from normality (Grossman, Nickerson & Freeman, 1991). PCAs of both winter and summer water temperature data elucidated gradients of years with high vs low water temperatures, and in both cases, PC 1 explained a majority of variance in the data sets (winter 59%, summer 55%).

Consequently, annual scores from these components were used to represent the impacts of density-independent processes on population parameters.

Fish sampling

Brook trout were sampled each September via direct current electrofishing, and a complete description of sampling is provided in the study by Alexander & Nuhfer (1993). Length measurements were taken using a measuring board and means calculated for both the population and age classes. Population and age-class abundance estimates were made using the Peterson mark–recapture method with Bailey’s modification (Alexander & Nuhfer, 1993). Recapture sampling was conducted 2 days after the initial sampling. Abundance estimates were stratified by 25 mm length classes [total length (TL)] and representative scale samples taken from each size class for ageing analysis. These data were used to calculate the percentage of each length class composed of each age class, and abundance estimates were adjusted accordingly. We separated the population into young-of-the-year (YOY), 1+ (fish in their second year of life) and adult (2+ and 3+, fish in their third and fourth years of life) life-history classes, which together represented the vast majority of the population. Although brook trout occasionally reach age 6 in Hunt Creek (Alexander & Nuhfer, 1993), we did not include fish older than 3+ in population regulation analyses because their numbers were low, even in the Unfished Period, and hence, were less likely to have been adequately sampled in a consistent manner. In addition, when fishing was permitted, brook trout older than age 3 were highly exploited; hence, their inclusion would have biased our analyses. Abundance estimates were converted to density (fish per m²) using areal estimates of the study site (Alexander & Nuhfer, 1993).

Statistical analysis

Multiple factors may affect population processes in animals (Hixon, Pacala & Sandin, 2002; Grossman *et al.*, 2006), so we constructed a set of a priori models that included the effects of simple, complex and delayed density dependence, positive and negative density-independent effects, recruitment limitation, as well as combinations of these factors (Table 1). Following Burnham & Anderson (2002) and Grossman *et al.* (2006, 2010), we used regression analysis combined with information theoretical statistics to compare the explanatory power of these competing hypotheses. We used linear regression to assess the predictive power of models and regressed

models (Table 1) against both the *per capita* rate of increase [$r = \ln(N_t/N_{t-1})$] and growth (mean annual TL) of the population, adults, 1+ and YOY population segments. We evaluated the comparative explanatory power of each model using Akaike’s Information Criterion for small sample sizes – AICc, Δ AICc and Akaike weights (i.e. w_i values) (Burnham & Anderson, 2002; Grossman *et al.*, 2006, 2010). We assumed that changes in mean annual lengths represented differences in growth among years, but for adults it may also represent a difference in the ratio of older to younger adults because survivorship changed over years. Akaike weights represent the amount of information lost from the original data when using a given model as a representation of the data and range from zero to 1.0. A w_i of 1.0 means that no information is lost from the original data, when that model is used as a representation, whereas a value of zero indicates a complete loss of information. Following Burnham & Anderson (2002), we only interpreted explanatory models with w_i values equal to or >10% of the value of the best model and calculated model parameter estimates and 95% confidence intervals using the methods of Grossman *et al.* (2006). We calculated the comparative explanatory power of each model by dividing the w_i value of the best model by that of each remaining interpretable model, and this yielded a probability value that, given the data, the model being compared was X times as likely to be true as the best model (Burnham & Anderson, 2002; Grossman *et al.*, 2006, 2010). Concomitantly, Motulsky & Christopoulos (2004) have shown that if two models have a Δ AIC values of 2, then the best model is 75% more likely to be true, given the data than the model with the poorer fit, and for models with Δ AIC of five, this value jumps to 90%. Finally, although calculating the *per capita* rate of increase for population segments rather than for just the whole population may be a matter of contention, the calculation of such relationships is not inappropriate statistically and may yield important biological insights into population dynamics (Fryxell & Lundberg, 1998; Grossman *et al.*, 2006, 2010).

Models with the greatest explanatory power had high w_i values and parameter estimates that did not overlap zero. We also interpreted models with parameters whose confidence intervals overlapped zero, although we gave these models lower credence (Grossman *et al.*, 2006). Time series of abundance estimates is known to typically contain serial correlations and hence may be problematic for tests of density dependence (Dennis & Otten, 2000). The use of the *per capita* rate of increase rather than abundance values reduces this problem (Grossman *et al.*, 2006) but the strongest evidence for density dependence

Table 1 AIC models for *per capita* rate of change and standard length (TL) analyses. Models were derived from previous studies (Grossman et al., 2010) or the literature

Explanatory mechanism	Model	Response variable	Variables in candidate models
Global model	All variables		
Simple density dependence (DD): <i>per capita</i> rate of change for life-history class is limited by the density of that or another life-history class. Mechanism is intraspecific competition for food or habitat.	$r \text{ pop} = -f(\text{dpop}_t)$	rpop, radult, r1+, ryoy	-dpop - dadults, r1+, -dyoy
Delayed simple density dependence (DDD): <i>per capita</i> rate of change is limited by density of that or another life-history class in the previous year.	$r \text{ pop} = -f(\text{dpop}_{t-1})$	rpop, radult, r1+, ryoy	-dpop - radult _{t-1} , -ryoy _{t-1}
Complex density dependence (CDD): <i>per capita</i> rate of change is limited by density-dependent interactions with multiple life-history classes.	$r \text{ pop} = -f(\text{dpop}) + f(\text{dYOY})$	rpop, radult, r1+, ryoy	-dpop -radult, -radult _{t-1} , -ryoy, -ryoy _{t-1}
Simple negative density independence (DI): Negative relationships between r and temperature or flow limit <i>per capita</i> rate of increase for population. Positive density-independent effects also can be identified.	$r \text{ pop} = -f(\text{WTC1})$	rpop, radult, r1+, ryoy	-WTC1, -STC1, -WFC1
Complex negative density independence (CDI): Negative relationships between r and multiple physical factors limit <i>per capita</i> rate of increase for population. Positive density-independent effects also can be identified.	$r \text{ pop} = -f(\text{WTC1}) + -f(\text{STC1}) + -f(\text{WFC1})$	rpop, radult, r1+, ryoy	-WTC1, -STC1, -WFC1,
Recruitment limitation (RL): <i>per capita</i> rate of increase is limited by density of younger age class at time t.	$r \text{ adult} = f(\text{d1+}_{t-1})$	rpop, radult, r1+,	dyoy _{t-1} , d1+ _{t-1}
Complex multimechanism models (MM): Multiple mechanisms affect <i>per capita</i> of increase	$r \text{ pop} = f(\text{WFC1}) + f(\text{WTC1}) + -f(\text{dpop})$	rpop, radult, r1+, ryoy	-dadult, -dadult _{t-1} , -dyoy, -dyoy _{t-1} , -WTC1, -STC1, -WFC1, etc.

dpop = population density, WTC1= score on component one of PCA of winter temperature data, STC1= score on component one of PCA of summer temperature data, WFC1= winter flow component one score.

in our analyses occurs when both *per capita* rate of change and growth data display strong density dependence.

Results

Flow

Principle component analyses extracted two components with eigenvalues >1.0 that explained 85% of the variance in flow data. These components identified gradients between years with high mean daily winter flows, high daily maximum and minimum flows and frequent high flow events, and years with an opposing suite of flow characteristics (Fig. 1). There were temporal differences in PC1 scores between the Fished and Unfished Periods with years during the Fished Period displaying significantly lower PC1 scores and hence lower mean and maximum flows and fewer high flow events than years during the Unfished Period ($t = 4.35$, d.f. = 49, $P \ll 0.0001$). There were no significant differences in PC2 scores between periods.

Temperature

Principle component analysis identified multiple components with eigenvalues >1.0 but the first two components extracted 87 and 90% of the variance in the data for winter (Fig. 2a) and summer (Fig. 2b) temperature time series, respectively. The gradient in summer temperatures contrasted years with warm summer stream temperatures vs years with cool summer stream temperatures. Winter stream temperature data displayed a similar gradient between years with warm mean, minimum and maximum daily water temperatures and an increasing number of minimum daily temperatures above 6.1 °C, and years with the opposite characteristics.

Population dynamics

Young-of-the-year densities varied several-fold and adult densities varied by an order of magnitude during the

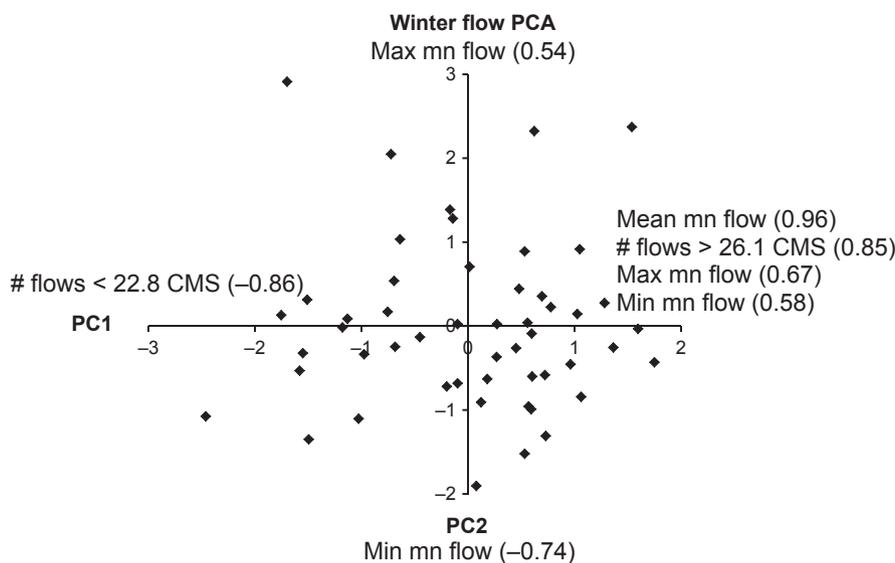


Fig. 1 First and second principle components for winter flow data (see Methods). Abbreviations are as follows: mn = mean, max = maximum, CMS = $\text{m}^3 \text{s}^{-1}$. Unless otherwise specified, values refer to daily flow estimates within a year (see Methods). Values in parentheses represent loadings for variables with loadings $> |0.40|$.

study (Fig. 3). Regression analysis did not detect a significant linear or nonlinear stock–recruitment relationship in any data set, although significance values for a positive linear relationship were 0.11 in the Unfished data set. Mean density and growth data displayed general trends consistent with exploitation effects as well as competitive release produced by the removal of large trout by angling. For example, mean densities of both the population and adults were significantly lower during the Fished than during the Unfished Period, and mean length of adults displayed the same relationship (Table 2). However, mean TL of both YOY and 1+ was significantly greater during the Fished Period, which is consistent with competitive release produced by reduced adult abundance during this period. There were no significant differences in the variances of density or mean length data between Fished and Unfished data, with the exception of adult density (Table 2). The variance of adult length was significantly greater in the Unfished Period than that in the Fished Period, which also is consonant with an exploitation effect.

Simple density dependence had strong explanatory power (i.e. w_i ; values 0.46–1.00) for *per capita* rate of change data for all demographic segments (15 of 16 cases) in all data sets (Table 3, Fig. 4, parameter estimates presented in Appendices 1 and 2): the only exception was adults in the Temperature data set (Table 3). In the latter case, the model with the greatest explanatory power was simple density independence via a negative relationship between *per capita* rate of change for adults and summer water temperatures (Fig. 5). Nonetheless, simple density depen-

dence also had explanatory power for this data set, although it was 4.1 times less likely, given the data, than the density-independent effect (Table 3). In several cases, more than one simple density-dependent model was interpretable (e.g. rpop for most data sets) and recruitment limitation (a positive relationship between *per capita* rate of change of 1+ fish and YOY density in the previous year) also displayed explanatory power for the *per capita* rate of change for 1+ trout in the Fished Period. These results all show powerful effects of density dependence on the *per capita* rate of change for all segments of this population even when fishing is occurring (Table 3). In addition, we detected strong density dependence during the Unfished Period, even though density-independent processes were stronger in this period (i.e. higher flows and higher numbers of high flow events). The reliability of our results should be correlated with the length of the time series and the effects of fishing; consequently, the most reliable results most likely come from the Unfished Period with the Pooled data set next, then the Temperature data set and finally the Fished Period.

Results for growth (mean TL) data were more variable, although there was still strong evidence (15/16 cases, w_i values 0.28–0.99) for density dependence in either simple or delayed forms (Table 3). In the Pooled data set, simple density dependence was the model with the greatest explanatory power (w_i ranging from 0.68 to 0.99) for population (Fig. 6), adult and YOY growth, whereas for 1+ fish, simple delayed density dependence (adult density in year $t - 1$) was the best and only interpretable model.

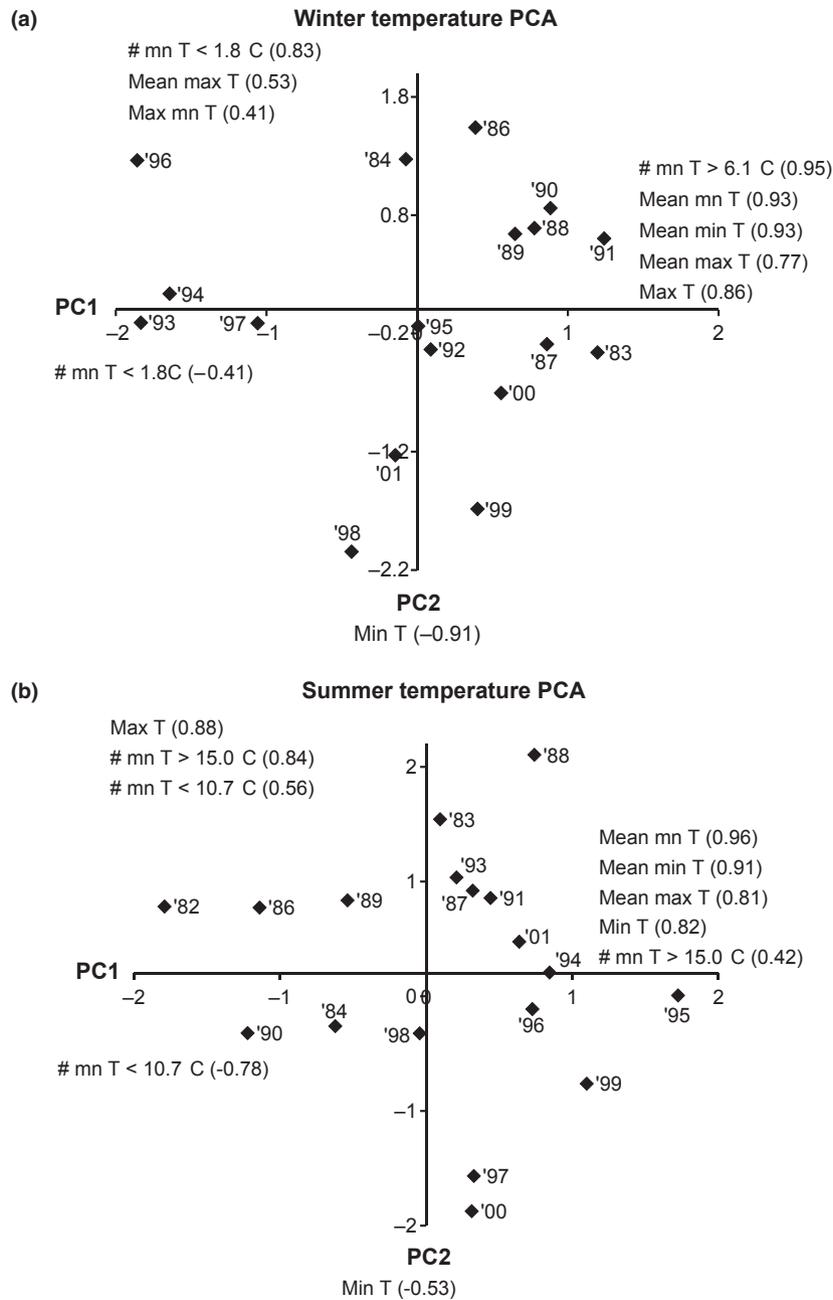


Fig. 2 First and second principle components for Winter (a) and Summer (b) temperature data for Hunt Creek. Abbreviations are as follows: T = temperature, mn = mean, max = maximum, Unless otherwise specified, values refer to daily temperature estimates within a year (see Methods). Values in parentheses represent loadings for variables with loadings > |0.40|.

The remaining models had much lower explanatory power (2.7–8.5X times less likely than the best model given the data) and also had parameter estimates whose 95% CI overlapped zero (Table 3). Model selection results for the Fished Period were similar, although all models had confidence intervals that overlapped zero, which lowers their explanatory power regardless of the w_i value (Table 3). In contrast to other population segments, adult growth in the Fished Period was best explained by three

equally probable models (Table 3) including (i) positive density independence (a positive relationship between mean TL and winter flows), (ii) simple density dependence and (iii) delayed positive density dependence (length was positively related to adult density in the previous year) which may represent a ‘carry-over’ effect of large adults displaying low mortality. Similar results, although in slightly different order, were observed for 1+ fish and YOY, although density independence and

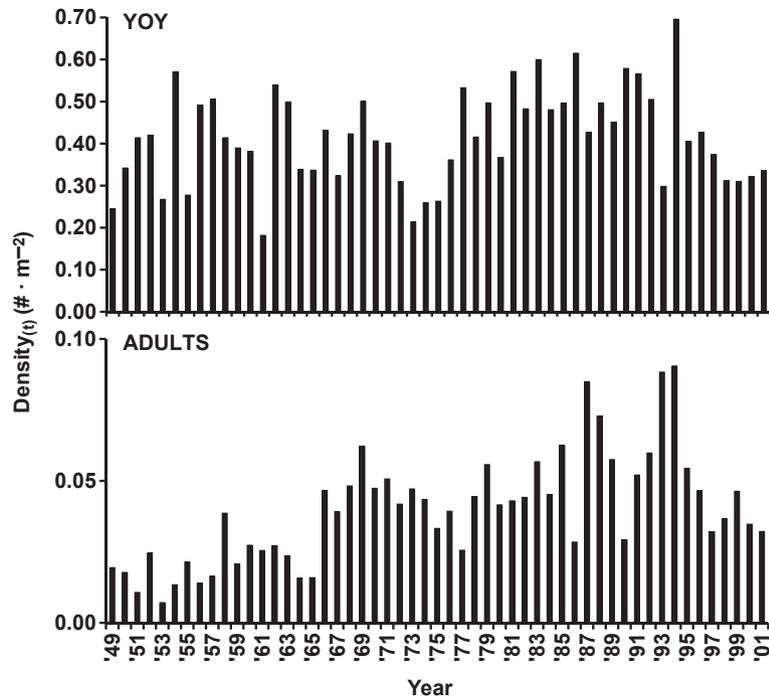


Fig. 3 Annual abundance estimates for young-of-the-year and adult brook trout from Hunt Creek 1949–2001.

Table 2 Significance tests for differences in density and growth

Population segment	Fished period ($\bar{x} \pm SD$)	Unfished Period ($\bar{x} \pm SD$)	Fished period variance	Unfished period variance
Density (# m ⁻²)				
Population	0.55 ± 0.13	0.63 ± 0.13*	0.0157	0.0169
Adult	0.02 ± 0.01	0.05 ± 0.02***	0.0001	0.0003**
1+	0.14 ± 0.05	0.15 ± 0.04	0.0023	0.0014
Young-of-the-year (YOY)	0.39 ± 0.11	0.43 ± 0.11	0.0120	0.0127
Mean total length				
Population	96.82 ± 6.34	97.79 ± 5.02	40.1817	25.1843
Adult	185.04 ± 8.29	191.82 ± 12.12*	68.6677	146.8944
1+	135.08 ± 4.64	131.57 ± 4.52**	21.5055	20.4105
YOY	78.55 ± 3.23	74.72 ± 3.47***	10.4381	12.0430

We only describe models for rpop, but similar models were run for each population segment and mean total length with the appropriate substitutions (e.g. DD – radult = –f(dadult), DD – mean TLpop = –dpop). Abbreviations are as follows: rpop = r for population, radult = r for adults, etc., FC1 = scores on flow PC1, WTC1 = scores on PCA of winter temperature data, STC1 = score on PCA of summer temperature data.

**P* < 0.05.

***P* < 0.01.

****P* < 0.001.

positive density dependence were much less likely than simple density dependence for YOY (Table 3). Growth relationships during the Unfished Period showed strong

simple density dependence for the population and adults, and parameters did not overlap zero (Table 3). Growth of 1+ fish in the Unfished Period was negatively related to summer water temperatures, with no other interpretable models (Table 3). Finally, YOY growth also was best explained by three equally probable models including positive density independence (positive relationship between flow and growth), and both simple and delayed density dependence (Table 3). Results for the Temperature data set were even more complex, and most interpretable single parameter models had 95% CIs that overlapped zero. As with previous results, simple density dependence had the greatest explanatory power for population, adult and YOY growth data (*w_i* ranging from 0.38 to 0.95), whereas simple negative density independence was the best model for the growth of 1+ fish (Table 3) and represented a negative correlation between mean TL and summer temperatures (Fig. 7).

Discussion

Density dependence, in various forms, clearly is the primary demographic process affecting trout density and growth in Hunt Creek. Strong evidence for density-dependent population regulation occurs when density dependence is found in both density and growth data, and we obtained this result for almost all population

Table 3 Candidate models with explanatory power for *per capita* rate of increase and growth (TL) data for the Hunt Creek brook trout population

Response variable	Candidate model (mechanism)	AIC _C	ΔAIC _C	w _i
<i>Per capita</i> rate of change				
Pooled data (1951–2001)				
Population	DD, rpop = -f(dpop)	9.93	0.00	0.63
	DD, rpop = -f(dYOY)	10.98	1.05	0.37 (1.7×)
Adults	DD, radult = -f(dadult)	82.63	0.00	0.97
	DD, r1+ = -f(d1+)	34.51	0.00	1.00
Young-of-the-year (YOY)	DD, rYOY = -f(dYOY)	46.13	0.00	1.00
Fished period (1951–65)				
Population	DD, rpop = -f(dpop)	25.47		0.84
	DD, rpop = -f(dYOY)	28.78	3.31	0.16 (5.2×)
Adults	DD, radult = -f(dadult)	48.04		0.96
	DD, r1+ = -f(d1+)	28.79		0.56
1+	RL, r1+ = f(dYOY)	29.31	0.57	0.42 (1.3×)
YOY	DD, rYOY = f(dYOY)	37.04		1.00
Unfished period (1966–2001)				
Population	DD, rpop = -f(dpop)	4.69		0.54
	DD, rpop = -f(dYOY)	5.14	0.45	0.43 (1.3×)
Adults	DD, radult = -f(dadult)	47.71		0.98
	DD, r1+ = -f(d1+)	35.10		0.98
YOY	DD, rYOY = -f(dYOY)	29.34		1.00
Temperature period (1982–2001)				
Population	DD, r pop = -f(dpop)	14.77		0.46
	DD, r pop = -f(dyoy)	14.86	0.09	0.44 (1.0×)
Adults	NDI, radult = -f(STC1)	40.37		0.74
	DD, radult = -f(dadult)	43.18	2.80	0.18 (4.1×)
1+	DD, r1+ = -f(d1+)	38.36		0.91
YOY	DD, rYOY = -f(dYOY)	29.02		0.94
Growth (mean total length)				
Pooled data (1951–2001)				
Population	DD, pop TL = -f(dpop)	321.64		0.99
Adult	DD, adult TL = -f(dadult)	400.10		0.68
	*DDD, adult TL = -f(adult _{t-1})	402.10	2.00	0.25 (2.4×)
	*DDD, adult TL = -f(WFC1)	404.46	4.37	0.08 (8.5×)
1+	DDD, 1 + TL = -f(dadult _{t-1})	310.97		0.98
YOY	DD, YOY TL = -f(dadult)	290.07		0.78
	*DD, YOY TL = -f(YOY)	293.96	3.89	0.11 (7.1×)
	*NDI, YOY TL = -f(WFC1)	294.13	4.06	0.10 (7.8×)

Table 3 (Continued)

Response variable	Candidate model (mechanism)	AIC _C	ΔAIC _C	w _i
Fished (1951–65)				
Population	*DD, pop TL = -f(dpop)	124.54		0.71
	*PDDD, pop TL = f(adult _{t-1})	127.30	2.76	0.18 (4.0×)
	*PDI, pop TL = f(WFC1)	128.33	3.78	0.11 (6.6×)
Adult	*PDI, adult TL = f(WFC1)	133.75		0.39
	*DD, adult TL = -f(dadult)	133.92	0.17	0.35 (1.1×)
1+	*PDDD, adult TL = f(adult _{t-1})	134.53	0.78	0.26 (1.5×)
	*DD, 1 + TL = -f(d1+)	117.55		0.48
	*PDDD, 1 + TL = f(adult _{t-1})	118.60	1.04	0.29 (1.7×)
YOY	*PDI, 1 + TL = f(WFC1)	119.00	1.44	0.23 (2.1×)
	*DD, YOY TL = -f(dYOY)	101.88		0.67
YOY	*PDI, YOY TL = f(WFC1)	104.54	2.65	0.18 (3.8×)
	*PDDD, YOY TL = f(adult _{t-1})	104.84	2.96	0.15 (4.4×)
Unfished (1966–2001)				
Population	DD, pop TL = -f(dpop)	223.24		0.97
Adult	DD, adult TL = -f(dadult)	274.48		0.98
1+	NDI, 1 + TL = -f(STC1)	219.63		0.97
YOY	*PDI, YOY TL = f(WFC1)	209.20		0.44
	*NDDI, YOY TL = f(adult _{t-1})	210.09	0.88	0.28 (1.6×)
	*DD, YOY TL = -f(YOY)	210.12	0.92	0.28 (1.6×)
Temperature (1982–2001)				
Population	DD, pop TL = -f(dpop)	127.38	0.00	0.54
	*DDD, pop TL = -f(adult _{t-1})	129.19	1.81	0.22 (2.5×)
	*NDI, pop TL = -f(WFC1)	129.79	2.41	0.16 (3.4×)
Adult	DD, adult TL = -f(dadult)	134.74	0.00	0.95
1+	NDI, 1 + TL = -f(STC1)	112.94	0.00	0.91
YOY	*DDD, YOY TL = -f(adult _{t-1})	110.54	0.00	0.38
	*NDI, YOY TL = -f(STC1)	111.84	1.30	0.20 (1.9×)
	*DD, YOY TL = -f(YOY)	112.43	1.88	0.15 (2.5×)
YOY	*NDI, YOY TL = -f(WTC1)	112.57	2.03	0.14 (2.7×)
	*NDI, YOY TL = -f(WFC1)	112.58	2.04	0.14 (2.7×)

The comparative explanatory power of each model is listed in parentheses after w_i. Models with an asterisk have lower explanatory power because their 95% CI overlapped zero. Process abbreviations are as follows: DD, simple density dependence; DDD, delayed density dependence; PDD, positive density dependence; PDDD, positive delayed density dependence; RL, recruitment limitation; NDI, negative density independence; PDI, positive density independence; NDDI, negative delayed density independence; PDDI, positive delayed density independence.

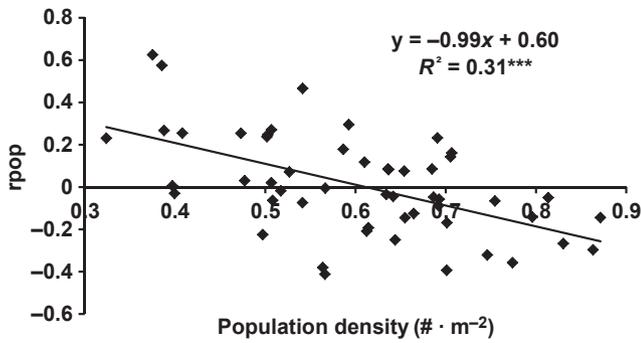


Fig. 4 Relationship between *per capita* rate of change of the population and population density for the Pooled data set (1950–2001).

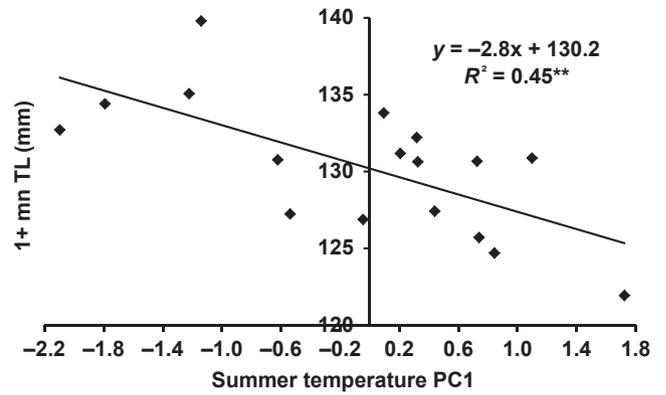


Fig. 7 Relationship between growth (mean annual total length, TL) of 1+ brook trout and PC1 score of the summer temperature principle component analysis (temperature data set, 1982–2001), * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

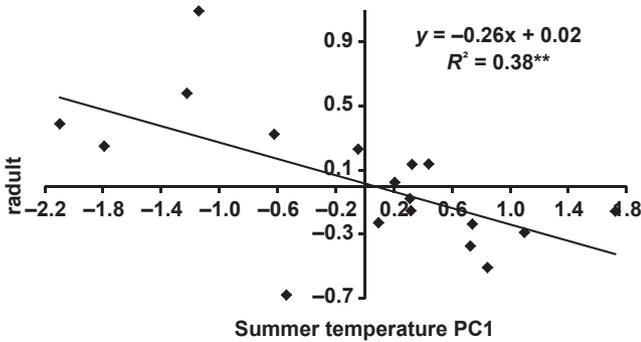


Fig. 5 Relationship between *per capita* rate of change for adult brook trout and PC1 score of the summer temperature principle component analysis (temperature data set, 1982–2001), * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

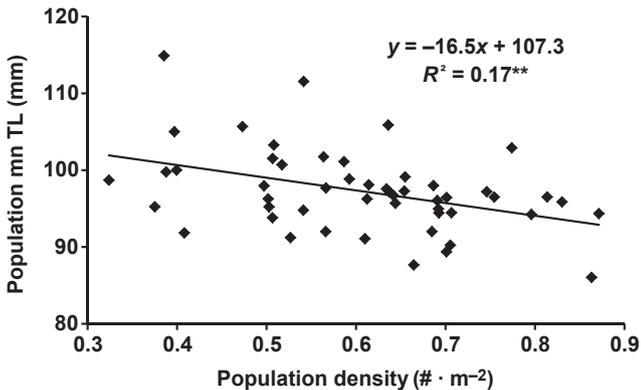


Fig. 6 Relationship between growth (mean annual total length, TL) of the population and population density for the Pooled data set (1950–2001), * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

segments in all time periods. Nonetheless, there were several interesting temporal patterns in the data. For example, during the Fished Period, none of the parameter estimates for interpretable growth models differed significantly from zero, which indicates that the strength of

density dependence was weaker during that period than in the Unfished Period. This result is consistent with known effects of exploitation; that reductions in density, especially of larger individuals, typically result in a release from intraspecific competition that most likely is the mechanism producing density dependence. In addition, density-independent effects on growth were observed in every population segment during the Fished Period, although these effects were weak for population data. Similarly, density-independent effects on growth also were documented when retrodicted temperature data were included in analyses, although this data set only included 20 years of data, and parameter estimates also frequently did not differ significantly from zero. Regardless of the data set, most density-independent models (i.e. temperature or winter flow) were 2–3 times less likely given the data than density-dependent models. Nonetheless, several of the patterns identified are consonant with what is known about brook trout biology (Grossman *et al.*, 2010).

The strongest form of density dependence is a simple relationship where a response variable is a first-order function of density. We detected a total of 44 models that involved density dependence, and of these, 35 were simple relationships, four involved delayed simple density dependence, and five involved positive density dependence in either simple or delayed forms. The latter relationships involve either carry-over effects or complex lagged relationships or represent Type I errors. Nonetheless, the vast majority of relationships involve simple density dependence, emphasising the importance of this process to population regulation in Hunt Creek brook trout. In addition, although its strength varied among data sets, we detected density dependence even when fishing

was significant or when Fished and Unfished data sets were pooled to form a 50-year time series. Consequently, the effect of exploitation between 1950 and 1965 was not strong enough to eliminate the effects of density dependence, although it did result in a reduction in its intensity. This contrasts with results from other trout populations where exploitation depressed population sizes sufficiently to make density-dependent effects undetectable (Almodovar & Nicola, 2004; Nicola *et al.*, 2008; Johnston *et al.*, 2007).

Our analysis does not address the mechanism of density dependence, although most likely it is intraspecific competition resulting in reduced growth and reproduction and ultimately either emigration or increased mortality. Density dependence in adult growth suggests that there will be less energy availability for reproduction and predator avoidance when brook trout density is high, which, in turn, suggests that compensation occurs through increased survivorship of younger age classes or decreased mortality. But density dependence in growth also was detected in YOY and 1+ growth, which suggests that both intracohort competition and intercohort competition are occurring, a phenomenon observed in both brook and brown trout (*Salmo trutta* Linnaeus) populations (Zorn & Nuhfer, 2007a; Kvingedal & Einum, 2011; Parra *et al.*, 2011; Lobon-Cervia, Budy & Mortensen, 2012).

Density dependence has been identified in other populations of brook trout, although its impact may be less than that for other trout species (Grant & Imre, 2005; Grossman *et al.*, 2010). The presence of density dependence in brook trout populations should allow them to recover from exploitation or environmental disturbance. Southern populations of brook trout frequently display little movement (Petty *et al.*, 2005; Hudy *et al.*, 2010), and populations may be maintained by a small subset of successfully reproducing adults (Hudy *et al.*, 2010). In regions where thermal conditions impose lesser constraints on brook trout movements (e.g. northern Michigan), brook trout may seasonally move 15 km or more within river drainages to utilise seasonally available thermal refuge habitats (Hayes *et al.*, 1998). Thus, the combination of flexibility in movement patterns and the presence of density dependence in this species may provide a biological safeguard for population persistence through time and at regional scales.

Stock–recruitment relationships provide strong evidence for density dependence, and positive linear stock–recruitment relationships have been identified in brook trout populations in Michigan, West Virginia and North Carolina (Petty *et al.*, 2005; Zorn & Nuhfer, 2007a; Grossman *et al.*, 2010). We failed to identify a significant stock–

recruitment relationship for any data set, although a positive linear relationship was significant at $P = 0.11$ in the Unfished Period. Stock–recruitment relationships are notoriously difficult to detect statistically, and many management plans just fit either a Ricker or Beverton–Holt stock–recruitment relationship to data and disregard statistical significance. Stock–recruitment relationships have proved particularly useful in evaluating the effects of density dependence in brown trout populations (Elliott & Elliott, 2006; Nicola *et al.*, 2008).

Density dependence in abundance, growth or survivorship also occurs in brook trout populations from Michigan (McFadden, 1961; Zorn & Nuhfer, 2007a), West Virginia (Utz & Hartman, 2009; Petty *et al.*, 2005) and North Carolina (Grossman *et al.*, 2010), although these relationships are not universal (Dunham & Vinyard, 1997; Grant & Imre, 2005). Of particular interest is the fact that brook trout densities in Hunt Creek Michigan and Ball Creek, North Carolina (Grossman *et al.*, 2010), display a several-fold difference in density, yet density dependence is the dominant regulatory process for both populations. Density dependence has been observed in several trout species including brown and golden trout Jordan (Elliott & Hurley, 1998; Knapp, Vredenburg & Matthews, 1998; Jenkins *et al.*, 1999; Kaspersson & Hojesjo, 2009), although it appears to be most common in YOY rather than adults (Elliott, 1994; Elliott & Elliott, 2006). Other investigators have failed to detect density dependence in brown trout populations (Elliott, 1994; Lobon-Cervia, 2007b; Nicola *et al.*, 2008), although there appears to be significant spatial variability in the operation of this process with nearby populations showing both evidence for and against density dependence (Lobon-Cervia, 2007b; Nicola *et al.*, 2008).

Our analysis represents one of the longest quantitative time series for a vertebrate species. Nonetheless, there are several shortcomings in our data set, most notably the lack of matching time series of environmental data. For both flow and Temperature data sets, we had to use correlation analysis to obtain sufficient data for analysis, and although correlations between flows in Hunt Creek and the Pigeon River were reasonable ($R^2 = 0.57$), this relationship was not as strong as we would have liked. Stochastic effects of flow on reproductive success have been documented in brown trout populations throughout their range (Strange, Moyle & Foin, 1992; Cattaneo, Hugueny & Lamouroux, 2003; Lobón-Cervía, 2004), and such effects appear to occur for both brook trout and brown trout in the relatively flat, hydrologically stable streams of Michigan (Zorn & Nuhfer, 2007b). The lack of significant flow effects on intrinsic rates of increase for

YOY brook trout in Hunt Creek may be a function of several features including (i) the quality of flow predictions used in the analysis, (ii) highly stable flow conditions in the headwaters of Hunt Creek or (iii) the fact that comparisons were made in autumn approximately 6 months after YOY emerged.

We correlated water temperatures at Hunt Creek and air temperatures at the Gaylord weather station, and these values were highly correlated ($R^2 \geq 0.90$). Nonetheless, we only used a data set of 20 years, because of concerns regarding well-known shifts in temperature relationship that have occurred over the last 50 years (IPCC 2008). In contrast to our findings of an inverse relationship between trout growth and summer temperatures in Hunt Creek, Hinz & Wiley (1997, 1998) observed a strong positive relationship between brook trout growth and summer water temperatures in northern Michigan streams, including Hunt Creek. There were a variety of methodological differences between the two sets of studies, however. First, Hinz & Wiley (1997, 1998) study was of much shorter duration (3 years) than ours and also Pooled data from multiple streams. Second, we defined summer temperatures as June through July, whereas the former studies used June through October as the summer period. Finally, we used correlative data to obtain water temperatures for half of our analysis and collapsed temperatures into a single mean for each year, whereas Hinz & Wiley (1997, 1998) had daily temperature measurements from each stream. Ultimately, we cannot determine whether these disparate results are a result of different biological processes operating over different time spans or in different populations, or from different methodologies. Nonetheless, Hinz & Wiley (1998) also found significant effects of density dependence on the growth of brook trout. Despite the shortcomings of our environmental data, they still produced interpretable models in several cases although density-independent processes never displayed the strength of density-dependent forces.

Alexander & Nuhfer (1993) examined the effects of fishing on brook trout demography in Hunt Creek using a subset of these data (1949–93). Some aspects of our results are similar and others differ. Like Alexander & Nuhfer (1993), we found that the main differences in density and growth between Fished and Unfished Periods occurred in the adult population segment, which was both significantly less dense and faster growing when fishing occurred. In addition, we both found that growth of 1+ brook trout was significantly lower during the Unfished Period, probably due to increased competition with larger trout that were more abundant during this period. We also observed this relationship in YOY. Alexander &

Nuhfer (1993) did not examine the role of density-dependent and density-independent factors on population change, but they did correlate survivorship with density and found a weak relationship between overwinter survivorship and density for YOY, although overwinter survival of older fish was not clearly related to density. Our results indicate that density dependence plays a stronger role in the dynamics of this species than previously thought.

The brook trout is the only salmonid native to inland waters of the eastern and mid-western United States. However, its status today is unclear because many natural populations have been extirpated (Hudy *et al.*, 2008). The population of brook trout in Hunt Creek displayed strong evidence of density dependence in both the *per capita* rate of increase and mean annual growth and provides one more example of the importance of this phenomenon in vertebrates. Nonetheless, it continues to be important to document the importance of density dependence in animal populations, because this process is the foundation of much of ecological and fisheries theory. The detection of density dependence in stream-dwelling populations of brook trout in geographically distant regions (Michigan, West Virginia and North Carolina) suggests that the importance of the process may be widespread and gives managers some confidence that these populations should be resilient after exposure to exploitation or natural or anthropogenic disturbances.

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Appendix 1

Parameter estimates for interpretable explanatory models for *per capita* rate of increase in trout population segments. Parameters with an asterisk had 95% confidence intervals that overlapped zero. Abbreviations are listed in Table 1.

Response variable	Regression parameter (b)	Estimate	95% CI
Pooled data (1951–2001)			
Population	–dpop	–0.99	–1.44 to –0.54
	–dyoy	–1.09	–1.60 to –0.58
Adults	–dadult	–10.06	–16.08 to –4.03
	–d1 +	–5.18	–7.13 to –3.24
Young-of-the-year (YOY)	–dyoy	–1.10	–2.72 to –1.27
Fished (1951–65)			
Population	–dpop	–2.19	–3.24 to –1.14
	–dyoy	–2.01	–3.20 to –0.81
Adults	–dadult	–53.37	–84.23 to –22.51
	–d1 +	–5.73	–9.09 to –2.36
YOY	dyoy	1.98	0.76 to 3.19
	–dyoy	–3.66	–5.23 to –2.09
Unfished (1966–2001)			
Population	–dpop	–0.67	–1.12 to –0.22
	–dyoy	–0.75	–1.27 to –0.23
Adults	–dadult	–12.24	–19.05 to –5.43
	–d1 +	–4.96	–7.39 to –2.54
YOY	–dyoy	–1.40	–2.13 to –0.67
Temperature data set (1982–2001)			
Population	–dpop	–0.80	–1.40 to –0.17
	–dyoy	–0.87	–1.55 to –0.20
Adults	–STC1	–0.29	–0.47 to –0.11
	–dadult	–11.34	–20.55 to –2.14
1+	–d1 +	–6.25	–9.88 to –2.63
YOY	–dyoy	–1.70	–2.72 to –0.69

Appendix 2

Parameter estimates for interpretable explanatory models for growth data for trout population segments. Parameters with an asterisk had 95% confidence intervals that overlapped zero. Abbreviations are listed in Table 1.

Response variable	Regression parameter (b)	Estimate	95% CI
Growth (mean annual total length)			
Pooled data (1951–2001)			
Population	–dpop	–20.12	–30.98 to –9.24
	Adults	–dadult	–167.36
	–dadult _{t-1}	–123.43	–280.29 to 33.43*
	WFC1	0.38	–2.84 to 3.60*

Appendix 2 (Continued)

1+	-dadult _{t-1}	-111.71	-173.61 to -49.82
YOY	-dadult _{t-1}	-56.68	-106.69 to -6.67
	-dyoy	-4.65	-13.88 to 4.59*
	-WFC1	-0.48	-1.52 to 0.57*
Fished (1951–65)			
Population	-dpop	-28.19	-56.73 to 0.34*
	dadult _{t-1}	215.41	-220.86 to 651.69*
	WFC1	0.25	-3.55 to 4.05*
Adults	-WFC1	-2.01	-6.56 to 2.54*
	-dadult	-211.87	-752.03 to 328.29*
	dadult _{t-1}	64.55	-490.51 to 619.61*
1+	-dy1	-38.03	-103.08 to 27.02*
	dadult _{t-1}	98.61	-227.81 to 425.04*
	WFC1	0.04	-2.75 to 2.82*
YOY	-dyoy	-11.73	-25.37 to 1.92*
	WFC1	0.46	-1.26 to 2.17*
	dadult _{t-1}	0.37	-206.00 to 206.74*
Unfished (1966–2001)			
Population	-dpop	-19.62	-30.92 to -8.33
Adults	-dadult	-516.23	-711.68 to -320.78
1+	-dadult _{t-1}	-125.51	-207.40 to -43.62
YOY	WFC1	0.76	-0.81 to 2.33*
	-dadult _{t-1}	-8.49	-79.645 to 62.68*
	Dyoy	0.74	-9.88 to 11.36*
Temperature data set (1982–2001)			
Population	-dpop	-25.40	-47.03 to -3.76
	-dadult _{t-1}	-131.72	-275.34 to 11.90*
	-WFC1	-4.17	-9.25 to 0.91*
Adults	-dadult	-381.95	-552.62 to -211.27
1+	-STC1	-2.93	-4.71 to -1.14
YOY	-dadult _{t-1}	-56.72	-136.93 to 23.49*
	-STC1	-0.73	-2.45 to 1.00*
	-dy1	-7.66	-45.81 to 30.48*
	-WTC1	-0.14	-1.770 to 1.50*
	-WFC1	-0.19	-3.16 to 2.78*