

Dynamics and regulation of the southern brook trout (*Salvelinus fontinalis*) population in an Appalachian stream

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SUMMARY

1. We used information theoretic statistics [Akaike's Information Criterion (AIC)] and regression analysis in a multiple hypothesis testing approach to assess the processes capable of explaining long-term demographic variation in a lightly exploited brook trout population in Ball Creek, NC. We sampled a 100-m-long second-order site during both spring and autumn 1991–2004, using three-pass electrofishing.
2. Principle component analysis indicated that the site had lower average velocity, greater amounts of depositional substrata and lower amount of erosional substrata during the 1999–2002 drought than in non-drought years. In addition, drought years had lower flows, and lower variation in flows, than non-drought years.
3. Both young-of-the-year (YOY) and adult densities varied by an order of magnitude during the study. AIC analysis conducted on regressions of *per capita* rate of increase versus various population and habitat parameters for the population, adults and YOY, for both spring and autumn data sets, indicated that simple density dependence almost always was the only interpretable model with Akaike weights (w_i) ranging from 0.262 to 0.836.
4. Growth analyses yielded more variable results, with simple density dependence being the only interpretable model for both adult spring data ($w_i = 0.999$) and YOY autumn data ($w_i = 0.905$), and positive density dependence ($w_i = 0.636$) and simple density independence ($w_i = 0.241$) representing interpretable models for spring YOY data.
5. We detected a significant stock–recruitment relationship between both spring and autumn densities of adults in year t and autumn YOY density in year $t + 1$. Finally, spring YOY density was positively correlated with both autumn YOY density and spring mean YOY standard length (SL), suggesting that processes affecting recruitment show residual effects at least in the first year of life. This population appears to be regulated primarily by density-dependent processes, although high flows also negatively affected mean SLs of YOY.

Keywords: density dependence, density independence, floods and droughts, long-term population studies, population regulation, stream fish

Introduction

Population regulation has been a topic of central interest in ecology for much of its history. Research on

this topic led to the early-mid twentieth century debate regarding the primacy of density-independent versus density-dependent factors in population control (McIntosh, 1985; Hixon, Pacala & Sandin, 2002). Given that animal populations frequently showed moderately bounded levels of variation, many researchers argued that density dependence must operate in these species (Murdoch, 1994; Hixon *et al.*, 2002). Nonetheless,

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populations of other species, especially insects and marine fish, varied over orders of magnitude, giving support to the density-independent school (Murdoch, 1994; Hixon *et al.*, 2002). At present, we recognise that population variation can be produced by many factors acting in concert or independently (Hixon *et al.*, 2002; Grossman *et al.*, 2006), although it has proved surprisingly difficult to detect the effects of density dependence on abundance variations in natural populations. A variety of factors have contributed to these difficulties including the following: (i) imprecision in sampling mobile organisms, (ii) the simultaneous actions of both density-independent and density-dependent forces on populations and (iii) difficulties in defining the spatial extent of populations. However, quantifying the factors responsible for population variation remains an important research topic, especially in the light of the increasing impacts of anthropogenic environmental change and its effects on species persistence.

Fishes have played a central role in studies of population regulation, because of their demographic characteristics as well as their economic importance. Fishes display a wide range of life history patterns (Matthews, 1998), which makes them an excellent group for comparative demographic analysis. In particular salmonids, a group with worldwide commercial importance, have been a focus for studies of population regulation, especially trout of the genera *Salmo*, *Oncorhynchus* and *Salvelinus* (Knapp, Vredenburg & Matthews, 1998; Jenkins *et al.*, 1999; Grant & Imre, 2005; Lobon-Cervia, 2007). Studies on salmonids suggest that density dependence operates primarily via mortality at high population density, whereas, at low density its primary effect is on growth (Grant &

Imre, 2005; Lobon-Cervia, 2007). Nonetheless, these findings are complicated by a number of factors. First, there appear to be regulatory differences between migratory and non-migratory populations (Knapp *et al.*, 1998; Lobon-Cervia, 2007), and migratory populations also are subject to unmeasured selective pressures during the migratory portion of their lives. In addition, some salmonids such as brook trout (*Salvelinus fontinalis* Mitchell) do not necessarily display this shift in density dependence from growth to mortality as population size increases (see Fig. 1 of Grant & Imre, 2005). Consequently, further study is necessary to assess the impacts of density dependence on stream populations of salmonid fishes.

Stream fishes in general are useful test subjects for studies of population control because they commonly are subject to density-independent mortality in the form of floods and droughts. This is certainly true for southern Appalachian streams, where both forms of flow variability are not uncommon (Grossman *et al.*, 1998, 2006). In fact, many stream fish assemblages appear to be more strongly affected by density-independent forces than density-dependent processes such as resource limitation and interspecific competition (Matthews, 1998). Nonetheless, this does not preclude density dependence from operating on individual species populations. For example, in Coweeta Creek, North Carolina, Grossman *et al.* (1998) found little evidence that interspecific competition affected assemblage-level characteristics, such as species richness or shifts in the relative abundances of species. Instead, density-independent processes in the form of floods and droughts were the dominant factors affecting assemblage-level properties. Although the abundance of most species fluctuated

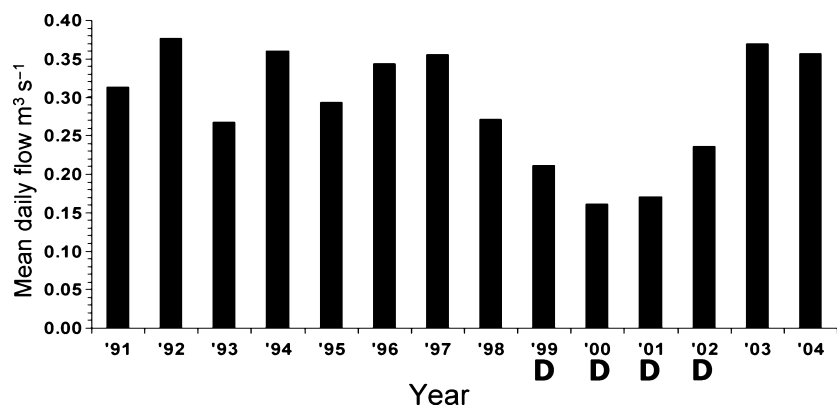


Fig. 1 Mean daily flows from weir 8 at the U.S.D.A. Forest Service Coweeta Hydrologic station for 1991–2004 (see Grossman *et al.*, 2006).

in concordance with these disturbances, the most abundant species, mottled sculpin (*Cottus bairdi* Girard), displayed an extremely stable population density throughout the 10-year multigenerational study. Subsequent research on three nearby sites in the same drainage demonstrated that density-dependent forces were the primary determinants of the muted population variation (typical coefficient of variation < 0.42) observed in mottled sculpin (Grossman *et al.*, 2006). Nonetheless, some demographic processes such as recruitment were strongly affected by density-independent processes, with recruitment positively correlated with flow in drought years and negatively correlated in years of normal or high flows (Grossman *et al.*, 2006). Although recruitment contributed little to overall population variation, these results illustrate the complexity of the causal forces affecting population properties in stream fishes.

With this in mind, we examined the effects of density-dependent, density-independent and recruitment-level processes on long-term population variation in a southern brook trout population in upper Ball Creek, NC, U.S.A. Specifically, we sampled a single permanent site biennially to quantify the density of the whole population and of adults and young-of-the-year (YOY) separately, over a 13-year period (three-four generations) and then calculated *per capita* rate of change (*r*) values for each segment of the population. We then constructed a series of mechanistic regression models capable of explaining variation in *r* and used Akaike's Information Criterion (AIC) to assess the relative ability of these models to explain the information content of the data (Grossman *et al.*, 2006). Finally, we performed the same analysis with growth data and also quantified a stock–recruitment relationship for this population.

Methods

The study species

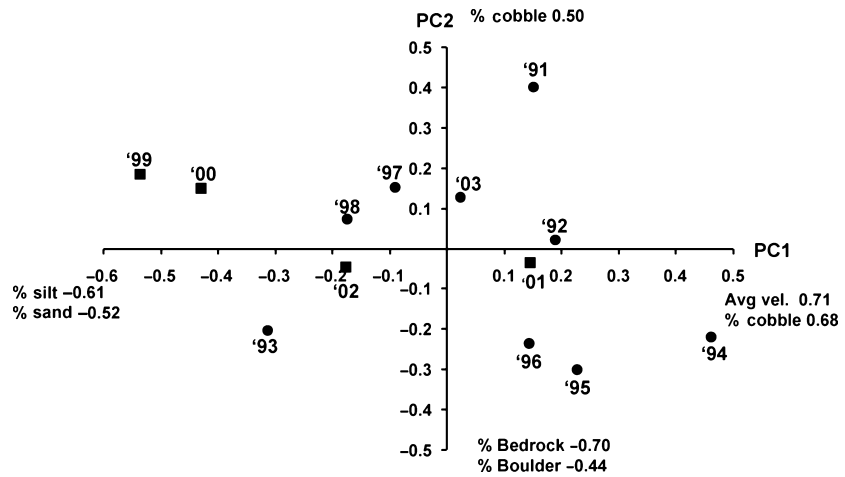
We chose southern brook trout as a study organism because little is known about its life history and population dynamics, and it is a species of concern to both aquatic ecologists and fisheries managers. Fixed genetic differences exist between southern and northern strains of brook trout, and these differences probably are sufficient to warrant taxonomic revision (Stoneking, Wagner & Hildebrand, 1981). Although

pure southern, pure northern and mixed populations of brook trout can be found in southern streams, the genetic identity of this population was confirmed by microsatellite analysis as pure southern brook trout (T. King, United States Geological Survey). Southern brook trout is the only salmonid native to the southern Appalachian Mountains and probably is a good indicator of water quality and general environmental conditions (Grossman *et al.* pers. obs). Typically, southern brook trout reach a small maximum size [<200 mm, standard length (SL)] and may live to 3+ years of age (Grossman *et al.* unpublished data, Stephen Moore, Nat. Park Serv. pers. comm.), although anecdotal records indicate that larger fish were common in the past. Nonetheless, brook trout in other areas of the United States display a similar life history pattern of moderate longevity (Petty, Lamothe & Mazik, 2005; Zorn & Nuhfer, 2007; Utz & Hartman, 2009), although this is not true for all populations. Also, Southern brook trout are of interest because it is possible that the range and population dynamics of this species will be affected by climate change (Flebbe, Roghair & Bruggink, 2006). Finally, southern brook trout exhibits readily separable YOY and adult life history classes, although in some years it is difficult to separate age groups within the adult segment of the population.

Study site

Our study site was a 100-m-long second-order section of Ball Creek, NC, U.S.A (~35.35°N by 83.25°W), similar to many streams that harbour brook trout populations in the southern Appalachians. Brook trout was the only fish species present in the site. The study site should have been of sufficient size to quantify population processes for this species based on previous population studies of other species in this system (Grossman *et al.*, 2006) and movement information on brook trout of similar size in other populations (Petty *et al.*, 2005). Bank side vegetation was dominated by rhododendron (*Rhododendron maxima* Linneaus) thickets, and the site was completely shaded during the growing season by overstorey trees typical of the local mixed hardwood – conifer forest. Our study period encompassed some of the highest stream levels on record over the last 60 years in the Coweeta Creek drainage (Fig. 1, Grossman *et al.*, 1998) and also included a harsh drought (1999–2002).

Fig. 2 Principal component analysis for autumn microhabitat availability data 1991–2003. Component loadings are listed after each variable. Component one contrasts years with high flows and erosional substrata versus years with the opposing suite of characteristics. Component two separates years with high amounts of bedrock and boulder and decreasing amounts of cobble from years with increasing amounts of cobble and little bedrock and boulder. Squares represent drought years.



Microhabitat availability

We collected data on physical microhabitat availability (*sensu* Grossman *et al.*, 1998, 2006), concurrently with spring and autumn population samples beginning in Autumn 1991 and ending in Spring 2004. Samples were collected when base flow conditions (flow levels typical for the period) had prevailed for 16 days prior to fish sampling, although in two cases longer intervals (19 and 30 days) were necessary either to match flow conditions or because of logistical difficulties. Logistical constraints also prevented us from sampling microhabitat availability data in spring 1992, 1996 and 1997; hence, most microhabitat analyses were based on autumn samples alone. We made microhabitat availability measurements at 1-m intervals on cross-stream transects, using the methods of Grossman *et al.* (1998). Transects were marked by stretching a tape measure between permanent bench marks placed at 5-m intervals along both banks. In brief, we measured depth (with a ruler ± 0.1 cm), mean current velocity ($0.6 \times$ depth, Marsh-McBirney Model 201 velocity meter ± 0.01 cm s⁻¹), and estimated substratum composition visually (% bedrock, boulders, cobbles, gravel, sand, silt, debris) at each metre mark. We also measured the wetted area of the site by using the transect lengths and the benchmark distances (5 m) as the edges of a quadrilateral and summing throughout the site.

We performed a principal component analysis (PCA, SAS Institute, 1985) on microhabitat availability data to document temporal changes in microhabitat availability. Principle component analysis is particularly suited for habitat analysis, because it identifies

correlated habitat variables and presents them as uncorrelated multivariate axes. Components with eigenvalues >1.0 that also represented ecologically meaningful patterns of variation were interpreted following Grossman & Ratajczak (1998). We also tested for differences in mean depth, mean average water column velocity and mean wetted width between drought and non-drought samples using a one-tailed *t*-test (hypothesising that drought values would be lower) or a Wilcoxon test. We have previously shown that null hypothesis testing is an appropriate approach for habitat availability, flow and microhabitat use data in this system (Petty & Grossman, 1996; Grossman & Ratajczak, 1998). We interpreted substratum loadings only if the original percentages differed by $>2\%$, our estimated observer error (Grossman & Ratajczak, 1998), unless their total composition was less than 10%. In all analyses, we set alpha to 0.1 to account for the following: (i) the inherent variability of long-term field data sets and (ii) the low sample sizes for drought data (e.g. $n = 4$), which we could not control.

Flow variation

We quantified the effects of density-independent factors (i.e. variation in stream flow) using flow measurements from stream gauges in both Ball Creek (Weir 9) and Shope Fork (Weir 8), the two primary tributaries of Coweeta Creek (Grossman *et al.*, 1998). Data from both weirs were used because they measure different hydrologic functions. Nonetheless, flows in the two streams are highly correlated (daily maximum flows – $r = 0.94$, $P << 0.01$, $N = 4212$; daily

minimum flows – $r = 0.98$, $P \ll 0.01$, $N = 4212$, Grossman *et al.*, 2006). The weirs provided the following data: (i) mean daily flow, (ii) minimum daily flow and (iii) maximum daily flow. From these data, we calculated maximum daily flow, minimum daily flow and mean daily flow for specific time periods (May–May, October–May, May–September and September–September). We also quantified the number of high flow events and the mean daily minimum flow during these time periods. Because the timing of high flow events determines their biological impact, we analysed flow data in concordance with the life cycle of brook trout and our sampling regime. Annual values for spring flow data were calculated based on a May–May water year, whereas annual values for autumn flow samples were based on a September–September water year. Specifically, we used data from the 12-month period before the spring or autumn fish sample, so there was some variation from year to year. Annual values were used for environmental analyses involving adults and autumn YOY, although environmental correlations with spring YOY were based on October–May data, because YOY only were spawned the previous autumn. We considered flows greater than $0.71 \text{ m}^3 \text{ s}^{-1}$ to represent ‘high flow events’ (see Grossman *et al.*, 1998), and this flow level had a recurrence interval greater than once per year (Grossman *et al.*, 1998). We also performed statistical tests on higher flows, specifically $1.4 \text{ m}^3 \text{ s}^{-1}$ and $2.1 \text{ m}^3 \text{ s}^{-1}$, but the results were very similar to those for $0.71 \text{ m}^3 \text{ s}^{-1}$, so only those data are presented. We tested for significant differences in the number of high flow events during drought and non-drought periods using a one-tailed *t*-test (fewer high flow events during the drought). This hypothesis was examined using both spring and autumn flow data sets.

We quantified the relationship between flow variation and the *per capita* rate of increase (r) of brook trout by first conducting a PCA on annual estimates of the 11 flow measures described earlier and then using the resulting scores for annual samples on these components in competing regression models (see Model Construction and Assessment).

Population sampling

We sampled the site between autumn 1991 and spring 2004, a period of extensive flow variation. Spring sampling ranged from 4 to 28 May and autumn

sampling from 23 August to 23 September (12 of the 13 were in September). Effort was kept constant among sampling occasions, and we used the sampling methodology of Grossman *et al.* (2006). We first placed block nets at the upper and lower boundaries of the site, anchored the lead lines using cobbles and then made three sequential passes through the site using a Smith-Root model backpack electrofisher. After each pass, fish were held in an aerated insulated container to prevent stress and measured (± 1 mm, SL) and weighed (± 0.01 g). Because samples generally were taken in the same month, comparisons of mean SLs actually represent growth trajectories of annual cohorts. After completion of the third pass, we replaced fish in the general location in which they had been captured.

We used a three-pass depletion estimator (Program Capture – White *et al.*, 1978) to derive abundance estimates for the population, YOY and adult (1+ and older fish) life history classes. Because juveniles (1+ individuals) are reproductively active in this and in other populations, including Appalachian streams (Hunt, 1969; Utz & Hartman, 2009), and are not always readily separable from older year classes on the basis of length, we combined them with adults into a single life history class. We used population estimates for all analyses except for one sample that yielded an unusually high population estimate. Observations while sampling indicated that this estimate was inaccurate (it was approximately twice the number of fish captured), so we derived a corrected total by adding the mean percentage of additional fish produced by Program Capture to the total number of fish captured in that sample. Peterson, Thurow & Guzevich (2004) have shown that sampling variance may result in an underestimate of the true population size when the three-pass depletion estimator is used. Nonetheless, sample variances were uncorrelated with sample means; hence, our estimates are probably reasonably accurate. In addition, mean wetted width varied by less than 0.5 m during the course of the study, and hence sampling efficiency should have been relatively equal among samples. Finally, we converted abundance estimates to densities using site wetted area measurements described previously.

Drought impacts were examined by comparing brook trout density estimates for drought and non-drought years with a one-tailed Wilcoxon test. Given the *a priori* expectation that drought is stressful, a null

hypothesis testing approach was appropriate. We also examined potential drought effects on the size–structure of brook trout populations by comparing mean length and mass values of YOY and adult brook trout in pooled annual samples from drought and non-drought years using a one-tailed t-test. Finally, we related various environmental and population parameters to the maximum size and density of large (>130 mm, SL) brook trout in samples using linear regression.

Model construction and assessment

Because both the literature and preliminary analyses indicated that multiple factors were capable of affecting variation in population parameters, we used a ‘strong-inference’ approach (see Burnham & Anderson, 2002 and Grossman *et al.*, 2006). We first constructed a series of *a priori*, mechanistic regression models that represented processes capable of explaining the information content of *per capita* rate of change ($r = \ln [N_t/N_{t-1}]$) or mean SL data for the southern brook trout population. These models included the following: (i)

density-dependent processes (negative relationship between density and r or SL, Table 1), (ii) density-independent processes (negative or positive relationship between physical habitat factors or flow and r or SL, Table 1) and (iii) recruitment limitation (positive relationship between r and density of a younger age class at time $t-1$, Table 1). We also examined more complicated candidate models, such as delayed density dependence and multifactor models (a complete description/specification of the candidate models is found in Table S1 and Grossman *et al.*, 2006). We then constructed a global regression model for the population, adult and YOY life history classes, which included all biologically relevant variables. Candidate models were fitted to the data (*per capita* rate of increase or mean SL) using linear regression (Neter *et al.*, 1996). The relative fit of these models was then evaluated using AIC adjusted for small samples (i.e. AIC_C, Burnham & Anderson, 2002). This metric measures the amount of information lost by using each candidate model, and the best fitting model has the lowest information loss (i.e. lowest AIC_C). We evaluated the ‘fit’ of competing models using their

Table 1 Explanatory models capable of explaining information present in the time series of r or growth values for the brook trout population and life history classes. To reduce redundancy, we only list models for the intrinsic rate of increase for the population, but similar models were run for each life history class and for growth data with the appropriate substitutions. A complete listing is provided in Table S1

Explanatory mechanism	Model	Response variable	Variables in candidate models
Simple density dependence (DD)			
Intraspecific competition for food or space limits <i>per capita</i> rate of increase of life history class	$r \text{ pop} = -f(\text{dpop}_t)$	rpop, radult, ryoy	-dpop -dadults, -dyoy
Simple density independence (DI)			
High, density-independent mortality produced by harsh conditions during high flow years limits <i>per capita</i> rate of increase for life history class.	$r \text{ pop} = -f(\text{PC1})$	rpop, radult, ryoy	-habpc1, -habpc2, -flowpc1, -flowpc2
High, density-independent survival produced by favourable conditions during high flow years limits <i>per capita</i> rate of increase of life history class	$r \text{ pop} = f(\text{PC1})$		habpc1, habpc2, flowpc1, flowpc2
Simple recruitment limitation (RL)			
<i>Per capita</i> rate of increase of adults is limited by density of YOY at time t	$r \text{ pop} = f(\text{dYOY}_{t-1})$	rpop, radult	dyoy _{t-1}
Complex multimechanism models (MM)			
Multiple mechanisms act independently on rate of increase in population or life history class	$r \text{ pop} = f(\text{PC1}) + f(\text{PC2}) + [-f(\text{dpop})] + f(\text{dYOY})$	rpop, radult, ryoy	-dadult, -dadult _{t-1} , -dyoy, -dyoy _{t-1} , -habpc1, -habpc2, -flowpc1, -flowpc2

Rpop, r for population; radult, r for adults; rYOY, r for young-of-the-year; dpop_{*t*}, population density in year t (dyoy, etc.); pc1, sample score on principal component 1; pc2, sample score on principal component 2.

Δ AIC weights (i.e. w_i values), which vary from 0 (complete information loss) to 1.0 (no information loss). The value of w_i represents the posterior probability that a candidate model is true, given the data and the competing candidate models (Burnham & Anderson, 2002). The information value of a competing model can be assessed by dividing the highest w_i value in the model set by the w_i value of that model (Grossman *et al.*, 2006). This yields the comparative likelihood that, given the data, the best model (highest w_i value) is true compared to any model with a lower w_i (Burnham & Anderson, 2002; Grossman *et al.*, 2006). Following Burnham & Anderson (2002), we only evaluated models with w_i values $\geq 10\%$ of the best fitting model. Although the validity of calculating r for subcomponents of a population (e.g., YOY) can be debated, there are no valid statistical reasons for not quantifying these relationships (see Fryxell & Lundberg, 1998), and they may identify variables that potentially affect these life history classes (Fryxell & Lundberg, 1998; Grossman *et al.*, 2006). We used a total of 13 candidate models, including the global model for *per capita* rate of change data, and a total of five candidate models for growth data.

Model-selection uncertainty was incorporated in our analyses by calculating model-averaged estimates (β , Burnham & Anderson, 2002) for individual coefficients (and standard errors) using Δ AIC weights (Grossman *et al.*, 2006). We estimated the relative importance of predictor variables by summing their Δ AIC weights over all interpretable models. We evaluated the interpretability of model-averaged coefficients by calculating 95% confidence limits for these coefficients using a *t*-statistic with $n-1$ d.f. Coefficients whose confidence limits included 0 were viewed as being uninterpretable.

Results

Habitat availability

During the study, physical habitat availability and flow varied significantly over both seasons and years (Figs 1–3). PCA for autumn habitat availability data indicated that the site had lower average velocity and cobble and more sand and silt during most of the drought (1999, 2000, 2002) and lower flow years (1993 and 1998) than in non-drought years (Fig. 2). The sample for the 2001 drought year

was grouped with non-drought samples probably because our sampling occurred shortly after a high flow event (pers. obs). Flow PCAs demonstrated that hydrologic variation was similar in both spring and autumn data sets, with drought samples displaying negative values (low flow characteristics) on PC1 and almost all non-drought samples exhibiting strong positive values (average to high flows; Fig. 3). Principal component 2 represented a gradient of years with low winter/spring and annual maximum flows and high summer flows versus years with high winter/spring and annual maximum flows and low summer flows (Fig. 3). There was little differentiation of drought and non-drought samples on component 2, and some of the highest and lowest scores on this component were for samples from drought years. Univariate analyses indicated that both mean average water column velocity (14 versus 16 cm s⁻¹, $P < 0.08$) and mean wetted widths (3.8 versus 4.2 m, $P < 0.03$) were significantly lower in drought years than in non-drought years. Mean depth did not differ significantly between drought and non-drought years. There were significantly fewer high flow events (i.e. > 0.7 m³ s⁻¹) during the drought (mean = 13.7) than in non-drought years (mean = 35.7, $P < 0.001$) and this was true for both winter/spring (November–May, drought 11.7, non-drought 29.4 *t*-test, $P < 0.009$) and summer data sets (May–September, drought 2.0, non-drought 7.0 *t*-test, $P < 0.019$).

YOY dynamics. Both YOY density (Fig. 4) and growth (i.e., mean SL) varied during the course of our study but there were no significant correlations between sampling year and YOY density. Densities of YOY were significantly higher during autumn in drought years (mean density 0.08 YOY m⁻²) than in non-drought years (mean density 0.03 YOY m⁻²; Wilcoxon test $P < 0.04$). There were no significant differences in the densities of YOY during the spring of drought versus non-drought years. Autumn YOY density was strongly correlated with Spring YOY density ($R^2 = 0.76$, $P < 0.001$), suggesting relative stability within this segment of the population during the summer. There were strong linear stock–recruitment relationships between both autumn (Fig. 5) and spring ($R^2 = 0.74$, $P < 0.001$) adult density in year t and YOY density in autumn of year $t + 1$. Variation in the YOY segment of the population was strongly

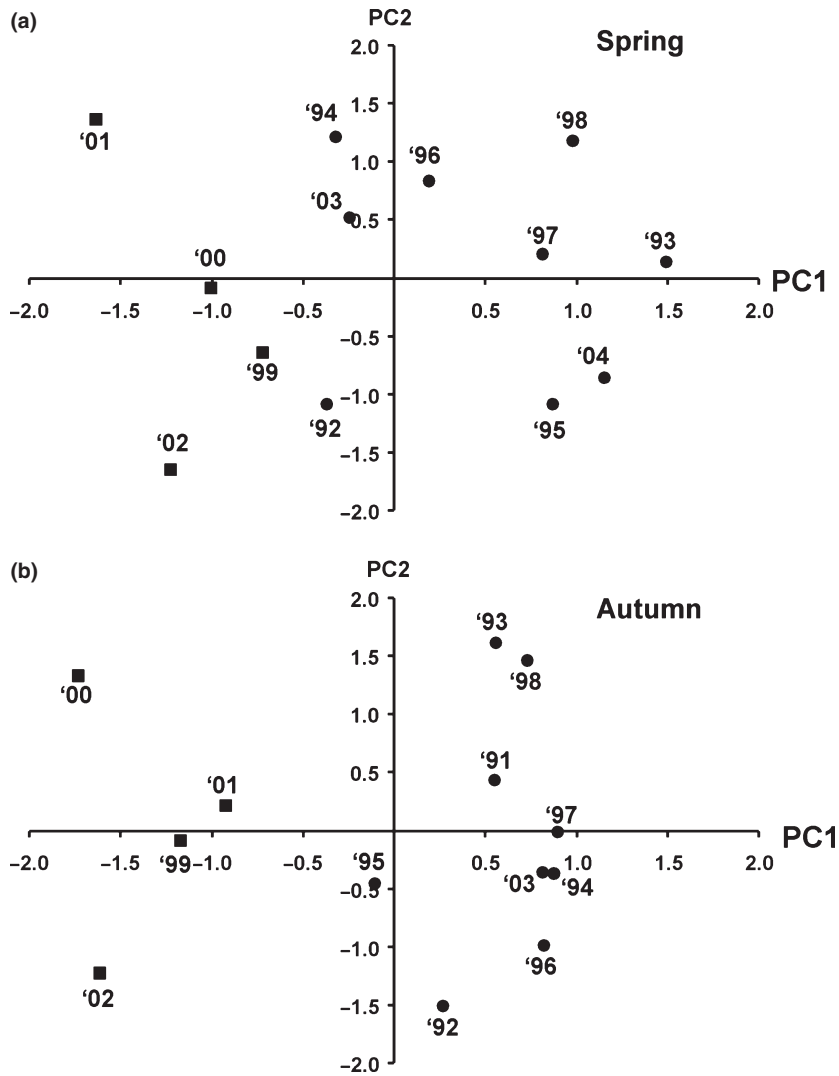


Fig. 3 Principal component analysis for flow data. Component loadings are listed below. Component one is a generalised flow gradient contrasting years with high and flow patterns (drought versus non-drought), and component two contrasts years with high winter and low summer flows versus years with low winter flows and high summer flows. (a) Spring flow period 1992–2004; (b) Autumn flow period 1991–2003. Closed squares indicate drought years, and closed circles indicate non-drought years. The loadings on the x-axis for the spring flow period are as follows: May_{t-1} to May_t mean flow 0.95, May_{t-1} to Sep_{t-1} number of high flows 0.91, May_{t-1} to May_t number of high flows 0.90, May_{t-1} to Sep_{t-1} mean min flow 0.88, May_{t-1} to Sep_{t-1} min flow 0.76, Oct_{t-1} to May_t number of high flows 0.73, May_{t-1} to May_t max flow 0.71, May_{t-1} to Sep_{t-1} max flow 0.68, Oct_{t-1} to May_t max flow 0.62; on the y-axis for the spring flow period: Oct_{t-1} to May_t max flow 0.65, Oct_{t-1} to May_t number of high flows 0.46, May_{t-1} to Sep_{t-1} max flow -0.56, May_{t-1} to Sep_{t-1} min flow -0.44. The loadings on the x-axis for the autumn flow period are as follows: Sep_{t-1} to Sep_t number of high flows 0.95, Sep_{t-1} to Sep_t mean flow 0.92, Oct_{t-1} to May_t number of high flows 0.86, Sep_{t-1} to Sep_t max flow 0.77, May_t to Sep_t min flow 0.68, Oct_{t-1} to May_t max flow 0.65, May_t to Sep_t max flow 0.61, May_t to Sep_t number of high flows 0.57; on the y-axis for the autumn flow period: Oct_{t-1} to May_t max flow 0.67, Sep_{t-1} to Sep_t max flow 0.43, May_t to Sep_t max flow 0.77, May_t to Sep_t min flow 0.53, May_t to Sep_t number of high flows -0.50.

affected by density-dependent factors, because simple density dependence [$r_{YOY} = -f(d_{YOY})$] was the only model capable of explaining variation in *per capita* rate of change data for YOY during both spring ($w_1 = 0.543$, Tables 1 & 2) and autumn ($w_1 = 0.836$, Tables 1 & 2, Fig. 6) sampling periods.

Both drought and seasonal variation affected growth attributes of YOY. Mean SL of YOY in autumn was not significantly correlated with mean SL of spring YOY. In spring, YOY were significantly longer during the drought than in non-drought seasons (drought mean SL = 41 mm, non-drought mean = 35

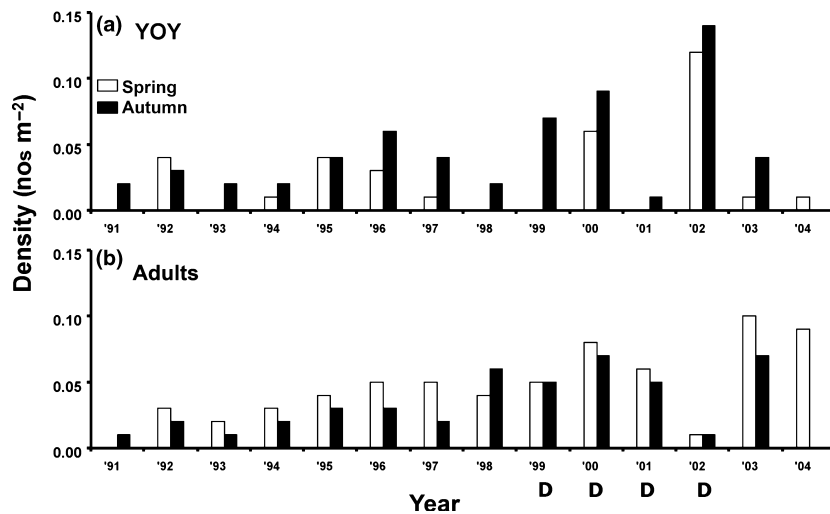


Fig. 4 YOY (a) and adult (b) densities for spring and autumn samples 1991–2004.

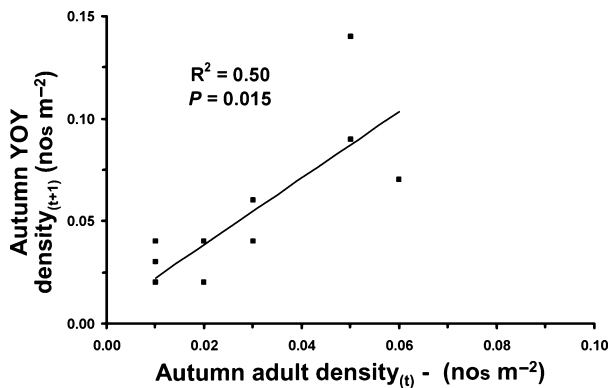


Fig. 5 Stock–recruitment relationship for autumn adult density (year t) and autumn YOY density (year $t + 1$).

mm, t -test = 5.35 $P = 0.0001$), although in autumn the opposite result obtained (drought mean SL = 59 mm, non-drought mean = 65; $t = -5.73$; $P = 0.0001$). Similarly, spring YOY were significantly heavier during the drought than in non-drought seasons (drought mean mass = 1.2 g, non-drought mean mass = 0.7; $t = 5.11$; $P = 0.0001$). In autumn, however, YOY were significantly lighter during the drought than in non-drought seasons (drought mean mass = 3.1 g, non-drought mean mass = 3.9 g; $t = -4.36$; $P = 0.0001$). Mean SLs of YOY were affected by both density-dependent and density-independent processes. The AIC analysis identified two interpretable models for the spring data; the first depicted a strong positive relationship between growth and YOY density (inverse density dependence, $w_i = 0.636$, Tables 1 & 2, Fig. 7a), and the second a weaker negative relation-

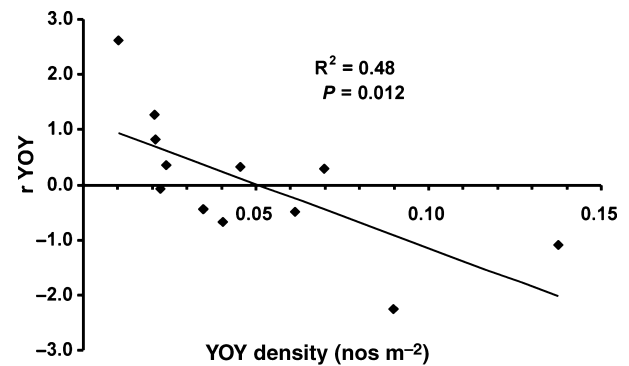


Fig. 6 Graph of the model with the greatest explanatory power given the data from AIC analysis (simple density dependence) for Autumn *per capita* rate of change data for YOY – $r\text{YOY} = -f(\text{YOY density})$. The relationships for other life history classes where simple density dependence was the only interpretable model for *per capita* rate of change data were similar, so this figure is presented as an example.

ship between high flows and growth (density independence, $w_i = 0.241$; Tables 1 & 2; Fig. 7b). Given the data, the former model was 2.6 times more likely to be true than the latter, but its interpretation is unclear, and it was strongly influenced by a single point (Fig. 7a). It is possible that the reduced number of high flow events during the drought produced both higher survival and growth and, hence, few effects of density dependence by spring. Nonetheless, in autumn, the only model capable of explaining information in YOY growth data was simple density dependence with population size ($w_i = 0.905$, Fig. 8). Given our sampling times, these findings suggest that

Table 2 Candidate models with explanatory power given the data. Akaike weights (w_i) were used to evaluate models. QAIC_c is Akaike's Information Criterion, and Δ QAIC_c is the change in AIC between subsequent models. Other abbreviations are as per Table 1. See for Methods further explanation

Response variable	Candidate model (mechanism)	QAIC _c	Δ QAIC _c	w_i	% max. w_i
Spring <i>per capita</i> rate of change					
Young-of-the-year (YOY)	Simple density dependence, $r_{YOY} = -f(dYOY)$	73.30	0.00	0.543	100
Adults	Recruitment limitation, $radult = f(YOY)$	50.32	0.00	0.594	100
Population	Simple density dependence, $rpop = -f(dpop)$	46.94	0.00	0.262	100
Autumn <i>per capita</i> rate of change					
YOY	Simple density dependence, $r_{YOY} = -f(dYOY)$	59.57	0.00	0.836	100
Adults	Simple density dependence, $radult = -f(dYOY)$	54.24	0.00	0.435	100
	Simple density dependence, $radult = -f(dadult)$	54.93	0.69	0.309	71 (1.4)
Population	Simple density dependence, $rpop = -f(dpop)$	43.67	0.00	0.443	100
	Simple density dependence, $rpop = -f(dYOY)$	43.93	0.26	0.389	71 (1.1X)
Spring mean standard length (SL)					
YOY	Inverse simple density dependence, $YOY\ SL = f(dYOY)$	87.63	0.00	0.636	100
	Simple negative density independence, $YOY\ SL = -f(PC1)$	89.58	1.94	0.241	38 (2.6X)
Adult	Simple density dependence, $adult\ SL = -f(dadults)$	105.56	0.00	0.999	100
Autumn mean SL					
YOY	Simple density dependence, $YOY\ SL = -f(dpop)$	90.43	0.00	0.905	100
Adults	No interpretable models				

density-dependent growth for YOY is most common during late spring and summer.

Adult and total population dynamics. Adult density also varied among years (Fig. 4), and both spring and autumn adult densities were positively correlated with sampling year (spring and autumn R^2 values were 0.33, $P < 0.05$), suggesting a trend for increasing density over time. Spring and autumn adult densities also were strongly correlated during the study ($R^2 = 0.80$, $P < 0.001$). As with YOY, this suggests that summer is a period of relative population stability. There were no differences in the density of adults in drought versus non-drought years, regardless of season. Spring and Autumn AIC analyses yielded different results (Table 2). In spring, the only interpretable model for adult *per capita* rate

of change was recruitment limitation [$radult = f(dYOY)$, $w_i = 0.594$, Fig. 9], although this relationship was strongly influenced by a single point. In autumn, however, there were two interpretable models with similar explanatory power and both represented aspects of simple density dependence [$radult = -f(dYOY)$, $w_i = 0.435$; $radult = -f(dadult)$, $w_i = 0.309$; Table 2]. Results for population *per capita* rate of change for spring indicated that simple density dependence was the only interpretable model [$rpopt = -f(dpop)$, $w_i = 0.262$], whereas autumn results for $rpopt$ were similar to those for $radult$, with two interpretable models [$rpopt = -f(dpop)$, $w_i = 0.443$; $rpopt = -f(dYOY)$, $w_i = 0.389$] with very similar amounts of information loss given the data (Table 2). Both models described simple density dependence with different population

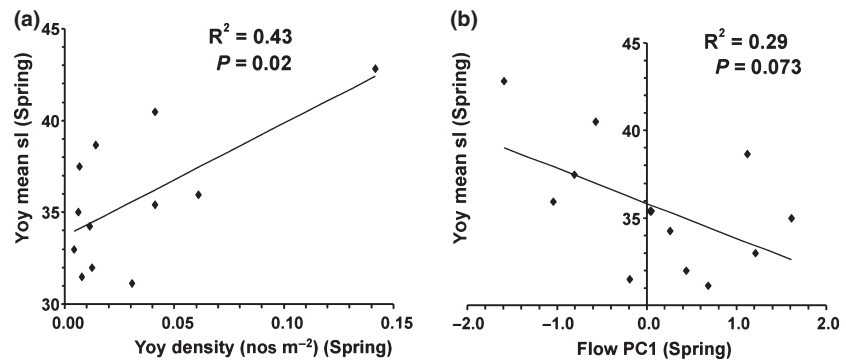


Fig. 7 Graph of the model with the greatest explanatory power given the data from AIC analysis for spring YOY mean SL data: (a) mean YOY SL versus YOY density; (b) mean YOY SL versus PC1 score.

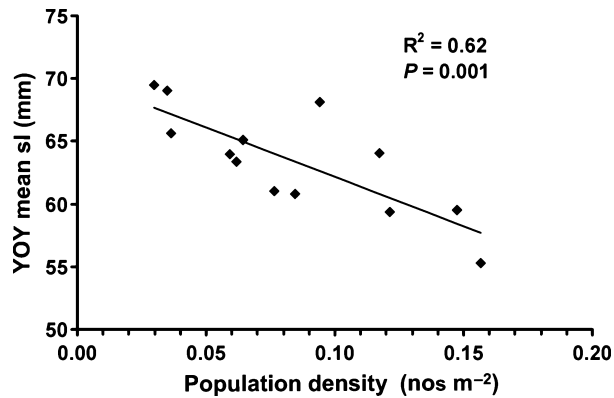


Fig. 8 Graph of the model with the greatest explanatory power given the data from AIC analysis for spring YOY mean SL data – versus population density. The relationships for other life history classes where simple density dependence was the only interpretable model for mean SL data were similar, so we did not present figures for these models.

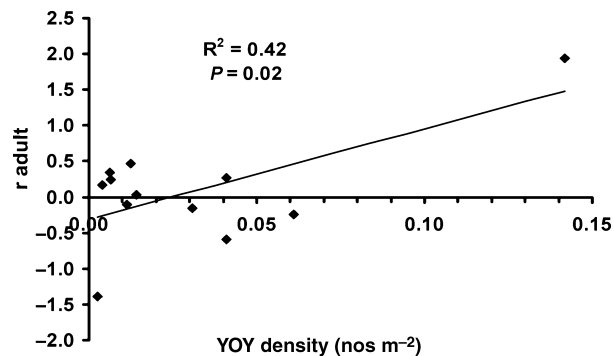


Fig. 9 Graph of the model with the greatest explanatory power (recruitment limitation, $r_{adult} = f(dyoy)$) given the data from AIC analysis for Spring *per capita* rate of change data for adults.

segments (adult density, $w_i = 0.483$; and YOY density, $w_i = 0.362$; Table 2). There were no significant differences in the density of large (>130 mm SL) southern brook trout between drought and non-drought periods, regardless of season, and no significant correlations between flow and the density of large southern brook trout. There were no significant correlations between adult or population density and either the maximum size or the density of large brook trout in spring or autumn samples.

Drought effects were also apparent in the adult segment of the population, because both adult length and mass were significantly lower during autumn of drought years than in non-drought years (drought mean SL = 109 mm, non-drought mean SL = 118;

t -test = -2.98 $P = 0.003$; drought mean mass = 18.5 g, non-drought mean mass = 24.5; $t = -3.02$; $P = 0.003$). There were no significant differences in either adult SL or mass for spring drought versus non-drought comparisons. Finally, spring and autumn adult growth analyses yielded differing results: spring adult growth was strongly affected by simple density dependence ($w_i = 0.999$), whereas all models for autumn adult growth data were uninterpretable because their parameter confidence intervals overlapped zero.

Discussion

Southern Appalachian streams are known for their low productivity (Whitworth & Strange, 1983; Cada, Loar & Slade, 1987; Utz & Hartman, 2006), and our results demonstrate that density-dependent processes affected both the *per capita* rate of change of both population segments as well as mean growth. In only two cases, spring adult *per capita* rate of change data and spring YOY growth data were models other than density dependence capable of explaining information in population data (Table 2). Nonetheless, because YOY abundance was primarily affected by density-dependent processes, the positive relationship between YOY abundance and spring adult *per capita* rate of change data ultimately is produced by density dependence (Table 2). Consequently, this population appears to be regulated by density-dependent forces acting on both adult and YOY density and growth. The presence of a positive linear stock–recruitment relationship for both spring and autumn adult densities also provides support for this conclusion, although densities never reached a level at which negative feedback occurred. It is unknown whether mortality or emigration is the density-dependent processes acting on *per capita* rate of change data. Nonetheless, the presence of density-dependent growth in spring adult samples implies that, when population density is high, mean adult size is low, which should result in lower fecundity and survival. The predominance of density-dependent forces is also somewhat surprising given the substantial environmental variation shown during the study. Nonetheless, similar patterns were observed in *C. bairdi* sampled in three nearby sites in the same catchment during different years (1984–1995) (Grossman *et al.*, 2006).

Spring and autumn densities of YOY and adults were highly correlated during our study, which suggests that mortality/emigration is not high during the summer. However, spring and autumn growth data for YOY were not significantly correlated, implying that density-dependent growth/emigration does operate during summer for this segment of the population. Several investigators have found that summer and autumn are seasons of low resource availability in Appalachian streams (Whitworth & Strange, 1983; Cada *et al.*, 1987; Ensign, Strange & Moore, 1990; Utz & Hartman, 2006) and, hence, possibly to be times when intraspecific competition occurs. An additional result that warrants discussion is the negative relationship between adult growth and density in spring. It is possible that this relationship was produced not by density dependence but by large numbers of small adults (1+ fish) in the population following high YOY survival the previous year. To test this hypothesis, we examined the relationship between YOY density in year $t-1$ (X) and mean SL of adults less than 110 mm SL in year t (Y). This produced a significant negative relationship ($r^2 = 0.39$, $P = 0.03$), indicating that growth was density dependent even in smaller adults. Finally, the finding of density dependence is supported by analyses of the *per capita* rate of increase for adults in Autumn.

Density dependence has been observed in brook trout populations in a variety of forms. Several investigators have identified stock–recruitment relationships for populations inhabiting Michigan and West Virginia streams (Petty *et al.*, 2005; Zorn & Nuhfer, 2007), and these relationships appear to be linear and similar in form to the stock–recruitment relationship for southern brook trout in Ball Creek. Brook trout survival was negatively correlated with density in all age classes (YOY, 1+ and 2+) in a Michigan River (Zorn & Nuhfer, 2007), and growth and density were negatively correlated for YOY (Zorn & Nuhfer, 2007). Density dependence also occurs in YOY in a different Michigan population (McFadden, 1961) and in several populations in West Virginia (Utz & Hartman, 2009). Finally, the strong correlation between invertebrate and brook trout production observed in a Minnesota stream also supports the contention that density-dependent processes are important to this species (Waters, 1982). Nonetheless, other studies have failed to demonstrate density-

dependent growth in brook trout populations (Dunham & Vinyard, 1997; Grant & Imre, 2005), and a lack of density-dependent growth relationships can be found in other salmonid species (Rincon & Lobon-Cervia, 2002; Arnekleiv, Finstad & Ronning, 2006; Lobon-Cervia, 2007).

Density-independent factors, especially high flows or droughts, also affect both brook trout and other salmonids. We detected several significant univariate correlations between high flow events and both density and growth within the Ball Creek population but, with one exception (spring YOY growth), their explanatory power was so low they were uninterpretable. Spring YOY growth data showed a significant positive relationship with density and a negative relationship with high winter flow. It is possible that this represents a situation where winter conditions typically are so harsh that, when the frequency of high flows decreased during the drought, brook trout responded positively in both survival and growth. However, by autumn, there was no apparent effect of high flow on YOY growth, and density was the only model capable of explaining information present in growth data. Multiple investigators have found that summer in Appalachian streams is a time of low food availability and potentially intense intraspecific competition for trout (Cada *et al.*, 1987; Ensign *et al.*, 1990; Utz & Hartman, 2006). Nonetheless, both droughts and floods can produce decreases in population size for trout in the Appalachians (Roghair, Dolloff & Underwood, 2002; Carline & McCullough, 2003; Hakala & Hartman, 2004).

Our results are unusual in that they demonstrate density-dependent effects for both YOY and adult trout. Density dependence has been difficult to detect in populations of mobile animals especially those with long life spans and complex life histories (Elliott & Hurley, 1998; Grossman *et al.*, 2006). In salmonids, there has been substantial debate regarding the role of density-dependent and density-independent factors on population variation (Lobon-Cervia, 2006, 2007). A variety of processes appear to affect the importance of density dependence in salmonids, including the amount of variation present within the population (Knapp *et al.*, 1998; Lobon-Cervia, 2006). However, there is much evidence for density-dependent growth in both stream-dwelling (non-migratory) and anadromous salmonid populations (Lobon-Cervia, 2006). In both kinds of population, density-dependent growth

appears to be most common (or most easily detected) in YOY, which may be a consequence of their relatively fast growth rates. The importance of density-dependent processes to adult salmonids is less well documented and evidence exists both for (Elliott & Hurley, 1998; Knapp *et al.*, 1998; Jenkins *et al.*, 1999; Zorn & Nuhfer, 2007) and against density dependence (Elliott, 1994; Lobon-Cervia, 2007). Elliott (1994) and Elliott & Elliott (2006) provided extensive evidence that density dependence only operated on YOY brown trout (*Salmo trutta* Linnaeus) in Black Brows Beck in the English Lake District and that adult population size was a function of the number of YOY surviving to adulthood, i.e. recruitment limitation (see Grossman *et al.*, 2006). However, density dependence was observed among adult brown trout in the nearby Wilfin Beck (Elliott & Hurley, 1998). Strong positive correlations between cohort density and adult density have been observed in several salmonid species including brook (McFadden, 1961), brown and golden trout (*Salmo aguabonita* Jordan) (Elliott, 1994; Knapp *et al.*, 1998; see review in Lobón-Cerviá, 2009).

Our results are based on long-term population data, although they are from a single site, albeit one that is apparently similar to many generally undisturbed streams in the region. One reason for our choice of this site was that it is very lightly or even unexploited (Grossman *et al.* pers. obs.), which means that it is unlikely that exploitation strongly affected our results. In addition, for several reasons demographic data suggest that our results have generality. First, the population structure of southern brook trout in Ball Creek resembled that of brook trout populations in other parts of the species' native range, with the exception that 2+ fish were somewhat smaller than those in Michigan (Zorn & Nuhfer, 2007) and West Virginia (Petty *et al.*, 2005). Nonetheless, this could have been because of the low productivity of southern Appalachian streams. In addition, Petty *et al.* (2005) showed that YOY and 1+ brook trout showed low movement rates in West Virginia, and these age classes dominated our population. Hence, it is unlikely that our results were strongly affected by fish moving in and out of our study site. Consequently, it appears that our results will be useful to other researchers in the southern Appalachian region.

In conclusion, our findings indicate that density-dependent processes are the primary forces determining population size and growth in a population

of southern brook trout. If true, this would enable southern brook trout to respond to environmental pressures via compensatory responses, which should increase their probability of persistence. One striking impediment to persistence of southern brook trout is low connectivity between populations. Petty *et al.* (2005) found that although YOY and 1+ brook trout showed little movement in West Virginia streams, older fish moved extensively among streams. These movements reduce genetic isolation and other negative population-level effects of habitat fragmentation. Larger streams in West Virginia provided suitable habitat for these movements, but larger streams in the southern Appalachians generally are too warm to support trout (Petty *et al.*, pers. obs). In particular, southern brook trout are typically restricted to headwater streams above barriers (e.g. waterfalls) and, where barriers do not exist, brook trout are eventually replaced by rainbow trout (Fausch *et al.*, 2001). Consequently, the prospect for genetic exchange among populations is greatly reduced, which will negatively affect their probability of persistence. Finally, southern brook trout are projected to decline in both abundance and distribution with climate change and future anthropogenic disturbance (Flebbe *et al.*, 2006; Hudy *et al.*, 2008). These factors suggest that the maintenance of high quality physical, thermal and biological habitat for southern brook trout may be the most effective means of ensuring their persistence.

Acknowledgments

We gratefully acknowledge the support of many students and staff who helped bring this research to fruition: Erin Dreelin, Mark Farr, Cathy Gibson, Anna, Rachel, and Barbara Grossman; Brett Henry, Kathleen McDaniel, Patricia Petty, Bridget Ratajczak, Pedro Rincon, Stacy Smith, Julie Stevens, Andrew Thompson and the staff of Jittery Joes and Two Story. In addition, long-term site access site and logistical support were provided by James Vose, and the staff of the U.S.D.A. Forest Service Coweeta Hydrologic Laboratory. This research was funded via long-term support from the U.S.D.A. Forest Service McIntire-Stennis program (grants GEO-0086-MS, GEO-00114-MS and GEO-00144-MS) and the National Science Foundation (BSR-9011661, DEB-9632854, DEB-2018001). Additional support was

provided by the Daniel B. Warnell School of Forest Resources. The manuscript benefited from the comments of Javier Lobon-Cervia, Stephen Moore, Gary Sundin and Ryan Utz.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Explanatory models capable of explaining information present in the time series of r values for sculpin population and life-history classes.

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(Manuscript accepted 27 October 2009)