Long-term persistence, density dependence and effects of climate change on rosyside dace (Cyprinidae)

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SUMMARY

1. We used long-term population data for rosyside dace (*Clinostomus funduloides*), a numerically dominant member of a stochastically organised fish assemblage, to evaluate the relative importance of density-dependent and density-independent processes to population persistence.

2. We also evaluated the potential impacts of global climate change (GCC) on this species and predicted how directional environmental changes will affect dace.

3. We sampled two 30 m permanent sites in spring and autumn in the Coweeta catchment for rosyside dace density using three-pass electrofishing between 1984 and 1995, and a single 100 m site from 1991 to 2003.

4. Habitat availability and flow variation data for this 20-year period demonstrated that two droughts (1985–1988 and 1999–2002) produced smaller wetted areas, lower mean, maximum and minimum flows, fewer high flow events and greater amounts of depositional substrata in the sites.

5. Droughts produced significant increases in abundance, and significant decreases in standard length and mass of rosyside dace. Increases in abundance were mainly due to increased survival/immigration of young-of-the-year (YOY).

6. Model selection analysis using multiple single and multivariable models indicated that density dependence in various forms possessed substantial explanatory power with respect to long-term variation in the per-capita rate of increase (r) in all sites and seasons. Density-dependent effects on r were stronger in autumn than spring, whereas negative density-independent models (flow variation) had the greatest explanatory power in spring.

7. Results for growth data were similar to those for rosyside dace density and confirm density dependence likely through intraspecific competition for food or foraging sites leading to reduced growth at higher densities.

8. These data support the hypothesis that species may persist in stochastic animal assemblages via strong intraspecific density dependence. Greater flow variability or increased high flows produced by GCC may destabilise this population leading to reduced compensation and possibly eventual extinction.

Keywords: assemblage regulation, compensation, density independence, intraspecific competition, stochastic theory

Introduction

We have entered a period in which environmental change is occurring at an accelerating rate. As a consequence, long-term studies of biological population are of special importance, because they document how populations potentially respond to both historic and future change. Population ecology is not a new field: indeed some of the earliest theories in this sub-discipline were developed at the beginning through the middle of the twentieth century during the debate over the relative importance of density-dependent and density-independent processes to population organisation (Andrewartha & Birch, 1954; Hutchinson, 1978). Nonetheless, similar

questions remain a central topic in modern population ecology and Sutherland *et al.* (2013) identified at least five fundamental ecological questions that require elucidation of the effects of density dependence in communities and populations. Not only is elucidation of the mechanisms determining population dynamics important for ecological theory but it also is essential for quantifying and predicting the effects of global climate change (GCC) on populations and ultimately on biodiversity. Finally, effective conservation strategies that consider GCC cannot be developed without knowledge of the forces determining population dynamics of species.

In this paper, we describe the relative importance of density-dependent and density-independent processes to long-term population dynamics of a numerically dominant member (rosyside dace, *Clinostomus funduloides*) of a stochastically organised fish assemblage inhabiting the Coweeta Creek catchment in North Carolina (Grossman *et al.*, 1998, 2010a). Because many of the species in the Coweeta Creek fish assemblage are on the southernmost end of their distributional range, they are excellent subjects for examination of how GCC may affect population dynamics over time. The Coweeta Creek catchment also likely is representative of many mountain stream systems in the southeastern United States (Grossman *et al.*, 2010a); the region with the highest biodiversity of freshwater organisms north of Mexico (Jelks *et al.*, 2008). In Coweeta Creek, fish biodiversity and resource use are most strongly correlated with flow variation coupled with species-specific responses to environmental change (Grossman & Ratajczak, 1998; Grossman *et al.*, 1998, 2010a; Grossman & Sabo, 2010).

Since we began quantitative assemblage sampling at Coweeta in the early 1980s, evidence has accumulated that both increased inter- and intra-annual environmental variability (for purposes of this study, environmental variability refers to interannual variability) and directional environmental change have occurred in the region: mean air temperatures and drought intensity show significant increases in both means and trends, and annual variability in precipitation has increased significantly since 1980 (Ford *et al.*, 2011; Laseter *et al.*, 2012). Our analysis of 77 years of flow data from the Coweeta catchment (Weir 8, 1935–2012) confirm the latter trend with 8 of the 10 lowest mean annual daily flows and 8 of the 10 highest mean annual daily flows occurring post-1980 (Grossman *et al.*, unpubl. data). These trends match regional patterns in precipitation observed by other investigators (Groisman *et al.*, 2004; Angert *et al.*, 2005; Laseter *et al.*, 2012). Given that there

has been little change in water temperatures from 1983–2012 (Grossman *et al.*, 2010a), long-term study of the Coweeta catchment fish should yield insights into how increased flow variation (density-independent forces), likely produced by GCC, may affect species.

Study species

Rosyside dace (Cyprinidae) is a numerically dominant member of the water-column habitat guild in the Coweeta catchment fish assemblage (Grossman *et al.*, 1998). Rosyside dace are distributed throughout the Atlantic Slope of the eastern United States, primarily inhabiting the Piedmont and Appalachian Mountain regions. This species possesses demographic characteristics similar to many members of the minnow family (Cyprinidae) including: (i) small adult size, maximum size about 90 mm standard length [SL], (ii) an intermediate life span reaching 5 years of age and (iii) populations dominated by adults (1+ and older) (Yanchis, 1993; Rincon & Grossman, 1998, 2001). Growth is fast in the first year of life, with young-of-the-year (YOY) quickly reaching a size that makes them indistinguishable from 1+ fish by late summer (Yanchis, 1993; Peoples & Frimpong, 2012; Grossman *et al.*, unpubl. data). Rosyside dace are drift-feeding insectivores that choose stream microhabitats based on maximising their net energy gain (Hill & Grossman, 1993; Grossman *et al.*, 2002). This species forms aggregations in favourable microhabitats, rather than shoals or schools, and their spatial dispersion within a stream reach is positively affected by eddies (Freeman & Grossman, 1992a,b; Freeman & Grossman, 1993). Although the majority of rosyside dace do not display intraspecific aggression, a minority are aggressive and have higher foraging rates and occupy more profitable foraging positions than non-aggressive individuals (Grossman & Boule, 1991; Freeman & Grossman, 1992b; Rincon & Grossman, 2001; Hazelton & Grossman, 2009). Mechanistically, intraspecific competition of this type could lead to strong density dependence within a population. Rosyside dace are good subjects for studies of population regulation, because many individuals display relatively small home ranges (20 m) and there is evidence of local population isolation (Hill & Grossman, 1987; White, 1988). Age 1+ fish are mature with a maximum fecundity of slightly less than 800 eggs and reproduction typically occurs in late spring to early summer (DeHaven *et al.*, 1992; Grossman *et al.*, 1998; Yanchis, 1993). Rosyside dace show seasonal changes in condition with winter being the season of poorest condition (Butler & Fairchild, 2005).

Members of the minnow family, including rosyside dace, are good subjects for studies of the effects of GCC on fish populations because they belong to the most speciose family of fishes in the world. Surprisingly, there are few long-term studies of population regulation in cyprinids despite their high species diversity and widespread distribution. Hence, studies that address the potential effects of GCC on members of this family should provide important contributions to conservation of this diverse family. Current research indicates that various aspects of minnow population dynamics, including growth and recruitment, are frequently affected by variation in factors likely to be affected by GCC including high and low flows on both a local and landscape scale (Wilde & Durham, 2008; Durham & Wilde, 2009a, b; Perry & Bond, 2009). Stream temperatures also affect the population dynamics of several common European minnows (Mills & Mann, 1985; Piffady *et al.*, 2010) and these temperatures may be influenced by marine phenomenon including spatial shifts by the Gulf Stream (Nunn *et al.*, 2007). Temperature effects would seem to be most prevalent among short-lived species, but they also occur in populations of long-lived minnows via formation of dominant year-classes (Mills & Mann, 1985).

Using the model selection approach of Grossman *et al.* (2006), we address the following specific questions: (i) what are the relative and combined importance of density-dependent and density-independent processes to long-term variation in the per-capita rate of increase (*r*) for rosyside dace populations?, (ii) what are the relative and combined effects of density-dependent and density-independent processes on mean annual growth of individual rosyside dace?, (iii) how similar are the long-term dynamics of rosyside dace populations along a short (~ 1 km) longitudinal stream gradient?, (iv) how likely is GCC to affect the processes determining population dynamics and individual growth in this species? and (v) how similar are the dynamics of rosyside dace populations to other members of the minnow family? For our evaluation of population processes, we put more emphasis on autumn data because it reflects the spring-summer growth period, whereas spring data likely better represent the effects of winter flows and reduced metabolic rates.

Methods

Site descriptions and sampling methodologies have been described previously (Grossman *et al.*, 2006, 2010a,b); hence, only the most relevant information is presented here.

Site description

Our data come from three sites where rosyside dace occur, along a short longitudinal gradient in the Coweeta watershed (~35.35°N, 83.25°W): Ball Creek and Coweeta Creek (BCB and CC of Grossman *et al.*, 2006) and Coweeta Creek 2 (CC2) located where Ball Creek and Shope Fork join to form Coweeta Creek (see Fig. 1 of Grossman *et al.*, 2010a). The latter site is the 'diversity site' of Grossman *et al.* (2010a). The sites were all within a 1 km reach and at an altitude of approximately 685 m a.s.l. (Grossman *et al.*, 2006). Two of the sites BCB and CC were 30 m in length and sampled between 1984 and 1995, whereas CC2 was 100 m in length and sampled between 1991 and 2004.

Habitat availability

Physical habitat availability data were collected from BCB and CC concurrently with fish sampling (see
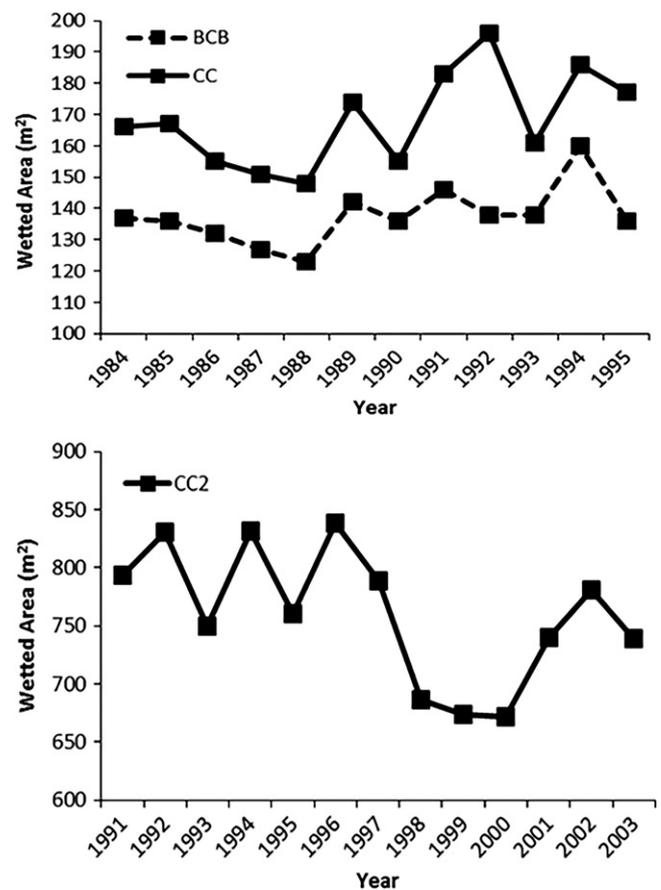

Fig. 1 Autumn wetted areas measured via transects for BCB, CC (1984–1995) and (CC2, 1991– 2004) (see Methods). Note difference in X axes.

below) beginning in autumn 1987 and ending in 1995 (1991 missed); however, because of missing data (1984–1987, 1991), these data were not used in population analyses (Grossman *et al.*, 2006). Grossman *et al.* (2006) showed that the main changes in habitat availability for BCB and CC occurred during the drought of 1985–1988, and involved shallower depths, lower mean velocities and decreased amounts of erosional substrata (Grossman *et al.*, 2006). Spring habitat availability data for CC2 also had too many missing values for inclusion in population analyses; hence the only habitat availability data included in population analyses, were autumn data for CC2. During this season, we collected 13 samples between 18 August and 10 October with nine collected during September. Habitat availability measurements were made via cross-stream transects, using the methods of Grossman *et al.* (1998). We located transects via permanent benchmarks at 5-m intervals along both banks. At each meter, we measured depth (with a ruler $\pm$ 0.1 cm), mean current velocity (0.6 X depth, Marsh-McBirney Model 201 velocity meter $\pm$ 0.01 cm s^{-1}), and estimated substratum composition visually (% bedrock, boulders, cobbles, gravel, sand, silt, debris) at each meter 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. Habitat availability data were analysed using by subjecting autumn habitat availability data to a principle component analysis (PCA) using the correlation matrix solution.

Flow variation

We quantified the effects of density-independent forces by measuring flow variation at gaging weirs eight and nine on the USDA Forest Service Coweeta Hydrologic lab. We used a series of flow measurements detailed below because they directly represent the hydrologic variability present in the system, and have yielded substantial insights into annual variations in flow in previous studies in the same system (Grossman *et al.*, 2006, 2010a,b). Daily, maximum and minimum flows from weirs eight and nine are both highly correlated with minimum *r* values of 0.93 (N = 4212) and measure different flow parameters (Grossman *et al.*, 2006). Flow measurements were described extensively in Grossman *et al.* (2006) for 30 m sites and in Grossman *et al.* (2010b) for 100 m sites; hence only a general description will be provided here. Briefly, for both data sets we conducted a PCA (correlation matrix solution) to determine patterns of annual variation in flow data using the

following flow data: (i) highest maximum flow during the year (calendar year), (ii) highest minimum flow during the year (calendar year), (iii) mean monthly flow (calendar year), (iv) mean monthly maximum flow (calendar year), (v) mean monthly minimum flow (calendar year), (vi) maximum flow between spring and autumn for a given year, (vii) maximum flow between autumn and the following spring, (viii) maximum flow between spring and the following spring, (ix) the number of high flows (see below) between spring and autumn of a given year, (x) the number of high flows between autumn and the following spring and (xi) the number of high flows between spring and the following spring. We classified drought and non-drought years based on flow patterns obtained via the PCA, as well as the 75+ year time series of mean daily annual flow data presented in Grossman, Ratajczak & Crawford (1995), Grossman *et al.* (2010a). Flow in years classified as drought represent some of the lowest mean annual daily flow values recorded continuously since 1935 Grossman *et al.* (1995, 2010a). Temperature differences between drought and non-drought years were minimal (Grossman *et al.*, 1998, 2010a).

Quantitative fish sampling

Rosyside dace were sampled bi-monthly from 1984–1987 (Freeman *et al.*, 1988) and twice annually (spring and autumn) from 1988–1995 in BCB and CC. The range of sampling dates for each site were as follows: BCB: spring samples, 28 April to 31 May, autumn samples, 16 August to 2 November (9 of 12 in September), CC: spring samples, 26 April to 25 May, autumn samples 19 August to 2 November (9 of 12 in September). A comprehensive description of sampling methodologies for BCB and CC is presented in Grossman *et al.* (2006). Sampling in CC2 was semi-annual (spring and autumn) and ranged in spring from 14 May to 6 June with 12 of 13 samples collected between 14 and 27 May and in autumn from 20 August to 1 October with 11 of thirteen samples collected between 9 and 19 September. Sampling periods for all three sites encompassed 3–5 times the mean generation time of rosyside dace. Fish were collected via three-pass electrofishing using a back-pack electrofisher (Smith-Root Model 11A electrofisher) and passes and total shocking time were of equal effort among samples. The site was blocked with 4.8 mm bar mesh seines prior to sampling. Mortality of dace was very low and all specimens were systematically distributed throughout the site after being individually weighed on an electronic balance ($\pm$0.01 g) and measured for standard length (SL $\pm$ 1 mm). Dace abundance

estimates were obtained via the three-pass depletion estimator of Program Capture (White *et al.*, 1982) and converted to densities using estimates of wetted width in the sites (methods of Grossman *et al.*, 2006, 2010b). We generally did not present results for young-of-the-year because they were inseparable $1+$ fish based on standard length (Yanchis 1993).

Population Processes

We constructed a series of mechanistic regression models capable of explaining annual variation in both the population (i.e. juveniles and adults) per-capita rate of increase ($r = \ln(\text{density}_{t+1}/\text{density}_t)$), and mean annual length (i.e. growth, Grossman *et al.*, 2006, 2010b) using spring and autumn samples. We then used Akaike's Information Criterion (AIC) to assess the relative ability of these models to explain the information content of the various models, given the data (Burnham & Anderson, 2002; Grossman *et al.*, 2006, 2010b). We first constructed a global regression model for the response variable of interest (r or mean SL) including biologically relevant variables (see below). Then we fit candidate models to the data (with linear regression (Neter *et al.*, 1996). The information loss incurred by using a given model was evaluated using Akaike's Information Criterion (AIC) adjusted for small samples (i.e. AIC_C, Burnham & Anderson, 2002), and the best fitting model has the lowest information loss (i.e. lowest AIC_C). Competing models were evaluated by comparing their ΔAIC weights (i.e. w_i values), which vary from 0 (complete information loss) to 1.0 (no information loss) (Burnham & Anderson, 2002; Grossman *et al.*, 2010b). W_i represents the posterior probability that a candidate model is true, given the data (Burnham & Anderson, 2002). The relative information contained in competing models is assessed by dividing the w_i value of the model with the highest w_i by the w_i value of any model with a lower value (Grossman *et al.*, 2006, 2010b). This yields a value that basically measures the information loss incurred by using a given model to explain the information content of the data, in comparison to the best fitting model and is expressed as 'model x is 3.5 times less likely to be true given the data than the best fitting model' (Burnham & Anderson, 2002; Grossman *et al.*, 2006). As per Burnham & Anderson (2002), we only evaluated models with w_i values ≥10% of the best fitting model. All calculations were performed in SAS (SAS Institute 1985).

We presented the candidate models in Grossman *et al.* (2006), but a brief description follows – not all models were used on all data sets because of data limitations (see above). We included both single and multivariable models including terms for: density dependence (X = density), density independence (X = annual values from the flow PCA), and habitat limitation (X = annual values from the autumn habitat PCA), delayed density-dependent and density-independent relationships and multi-variable models that included up to three of the five variables from single variable models. Because density at time t appears in both sides of the regression equation for per capita rate of increase (y) vs. simple density dependence (X), a finding of significance in such a model only is suggestive of a density-dependent effect (Grossman *et al.*, 2006, 2010b, 2012). However, findings of density dependence in growth data unequivocally demonstrate the presence of this process (i.e. density dependence) within a population, especially when per capita rate of increase yield the same result (Grossman *et al.*, 2006, 2010b, 2012).

We used univariate statistics to test for differences in abundance, mean standard length and mass between drought and non-drought seasons and among sites. Coefficients of variation were used to assess long-term abundance variations within and among sites over time and are based on autumn data. To test for temporal trends within data sets we compared early (BCB, CC1984-1989, CC2 1991-1997) vs. late (BCB, CC1990-1995, CC2 1998-2003) pooled years. Statistical tests were run using SAS (SAS Institute, 1985).

Results

Habitat variation

Autumn wetted widths for all three sites varied from high values in wet years to low values in drought years (1985–1988 and 1999–2002, Fig. 1). Values for CC2 ranged from 673–831 m^2, CC 148–186 m^2 and BCB 127–160 m^2, and both BCB and CC exhibited significantly smaller wetted areas in drought years than in non-drought years (BCB: $t = -2.99$, $P = 0.02$, CC: $t = -3.05$, $P = 0.01$), whereas values for CC2 only were significant at the 0.10 level ($t = -2.00$).

Flow variation

Despite the span of 20 years, flow variation in all three sites displayed similar patterns in both autumn and spring, with non-drought years generally displaying high mean, maximum and minimum flows, high mean minimum flows and higher frequencies of high flow events, regardless of season, than drought years (Fig. 2a,

b, 3a,b, Appendix 1). This pattern was weaker for spring data in BCB and CC where several non-drought years displayed negative values for PC1 (Fig. 3a). During spring in all sites, we identified a secondary pattern unrelated to drought that distinguished years with high autumn to spring, and annual maximum flows and high autumn to spring frequencies of high flows, from those with high summer maximum and minimum flows and high number of summer high flow events (CC2 only, 2a, b, 3a,b). A similar pattern was visible in autumn data for all sites, although it was less pronounced during drought years.

Habitat availability in CC2

Habitat availability in autumn in CC2 demonstrated that drought samples (1999–2002) displayed lower mean velocities, higher amounts of silt and lower amounts of cobble than most non-drought samples (Fig. 4). However, some non-drought samples displayed similar trends (1998, 2003), although those represent the years adjacent to drought years. Flow variability in both spring and autumn (Fig. 2a & b) showed similar trends: drought years had lower flows by virtually every metric examined (mean annual and seasonal flow, annual and seasonal minimum and maximum flows and number of annual and seasonal high flow events).

Population Processes

Density, drought effects and population variability. Dace density, mean standard length and mass varied over time in the three sites, and a clear pattern of increased densities during droughts was observed in all three sites (Figs 1 & 5, Table 1) regardless of the decade. The droughts of both 1985–1988 and 1999–2002 both
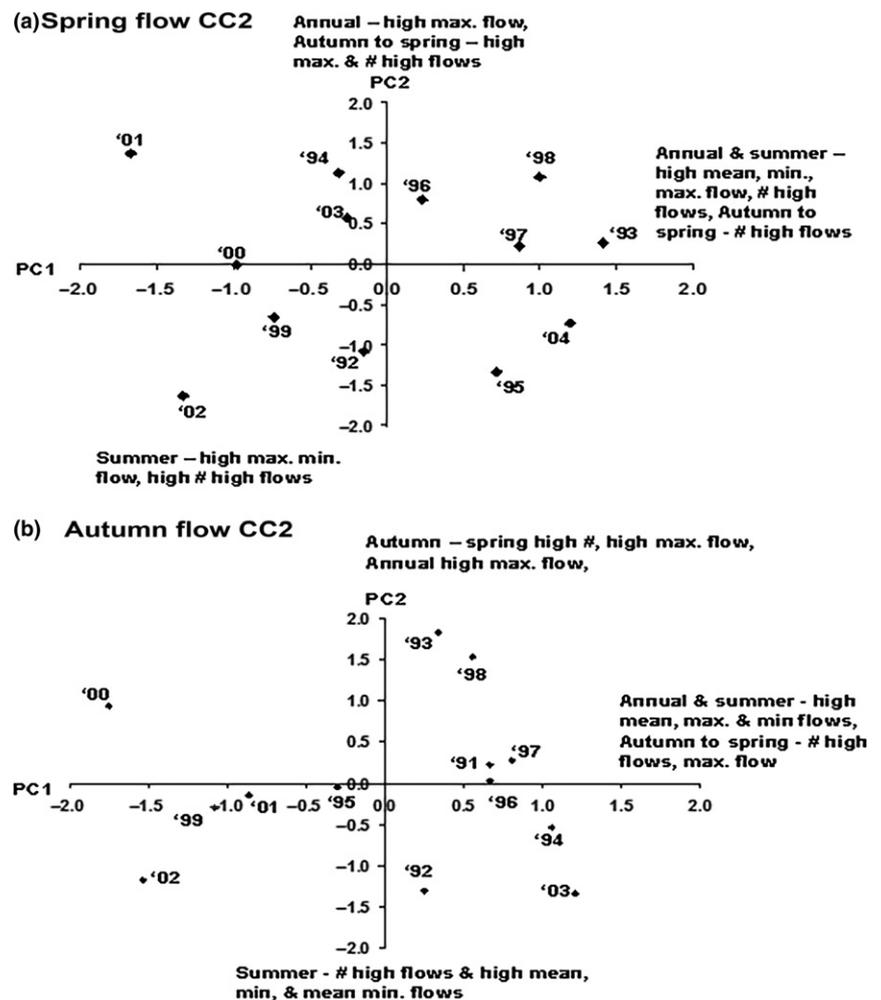

Fig. 2 Spring and autumn flow PCA's for CC2 (1991–2004). Variable loadings are presented in Appendix 1 (after Grossman *et al.*, 2010b).
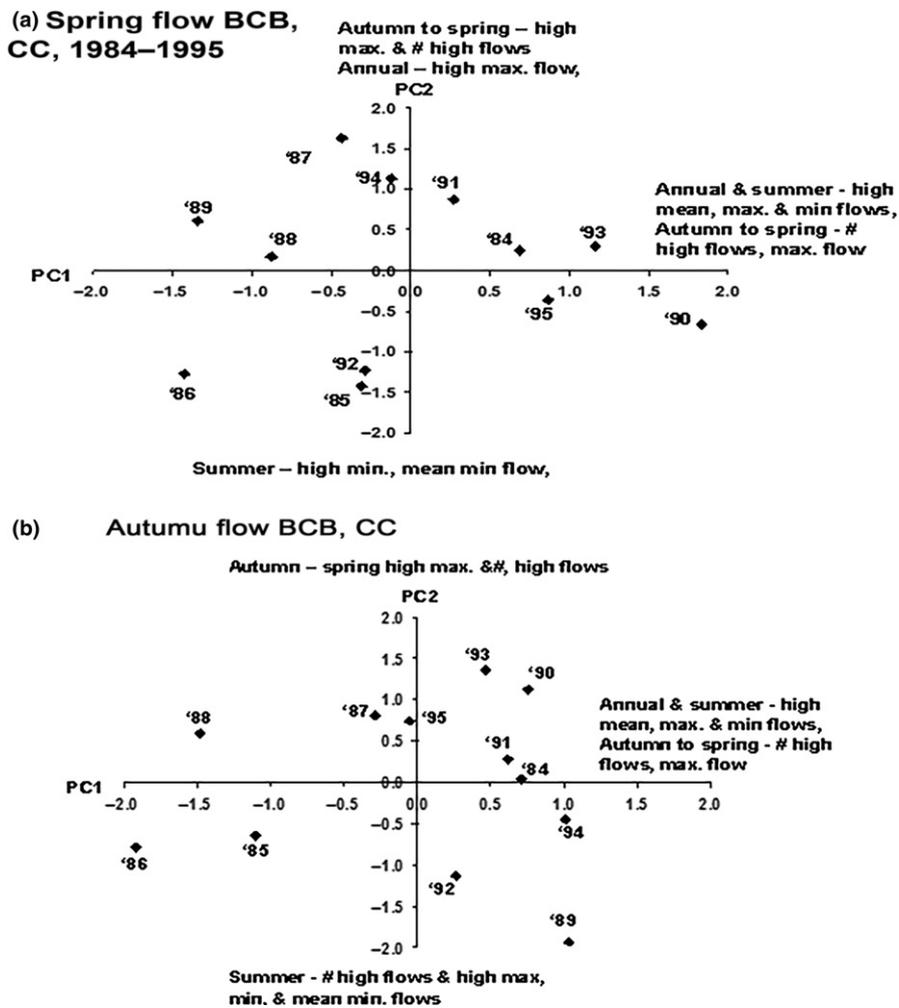
(a) Spring flow BCB, CC, 1984–1995

Autumn to spring – high max. & # high flows
Annual – high max. flow,

Annual & summer - high mean, max. & min flows, Autumn to spring - # high flows, max. flow

Summer – high min., mean min flow,

(b) Autumu flow BCB, CC

Autumn – spring high max. &#, high flows

Annual & summer - high mean, max. & min flows, Autumn to spring - # high flows, max. flow

Summer - # high flows & high max, min. & mean min. flows

Fig. 3 Spring and autumn flow PCA's for BCB and CC (1984–1995). Variable loadings are presented in Appendix 1 (after Grossman *et al.*, 2006).

significantly increased mean abundance of dace in CC during spring and autumn, in BCB in autumn, and in CC2 in spring (Table 1). In addition, there was a strong positive relationship between drought and the density of small dace (<50 mm SL, Fig. 6), most of which are YOY. Coefficients of variation (CV) for rosyside density estimates varied based on time period and drought vs. non-drought years but long-term trends were not apparent (Table 2). Values for CVs of population density ranged from 1.48 (BCB) to 0.52 (CC2), and were highest in 30 m sites which had lower mean densities than CC2. Both BCB and CC displayed higher CVs of density in early years which also included the drought (1985–1988, Table 2). However, in CC2 early years (non-drought) had a moderately higher CV than late years which included drought years 1999–2002 (Table 2). Drought vs. non-drought comparisons yielded slightly different results with BCB (30 m site) exhibiting a higher CV during the drought, than in non-drought years, likely due to a large increase in density during this period (Fig. 5).

whereas, both CC (30 m site) and CC2 (100 m site) displayed higher CVs of density in non-drought years. Consequently, there were no consistent relationships between CV of density and site size or mean density, mean standard length, or mean mass (Tables 1 & 2).

In contrast to abundance data, both mean SL and mass of dace decreased significantly in autumn samples from all sites but not in spring samples (Table 1). These differences were substantial with most differences in mass representing decreases of up to 25% in mass (Table 1) and support findings of density dependence given that dace were significantly more abundant during the droughts.

Population regulation

Per-capita rate of change. Model selection analyses indicated that dace density data exhibited density dependence, either in simple or delayed forms in all sites in all seasons, and Fig. 7 shows an example of simple
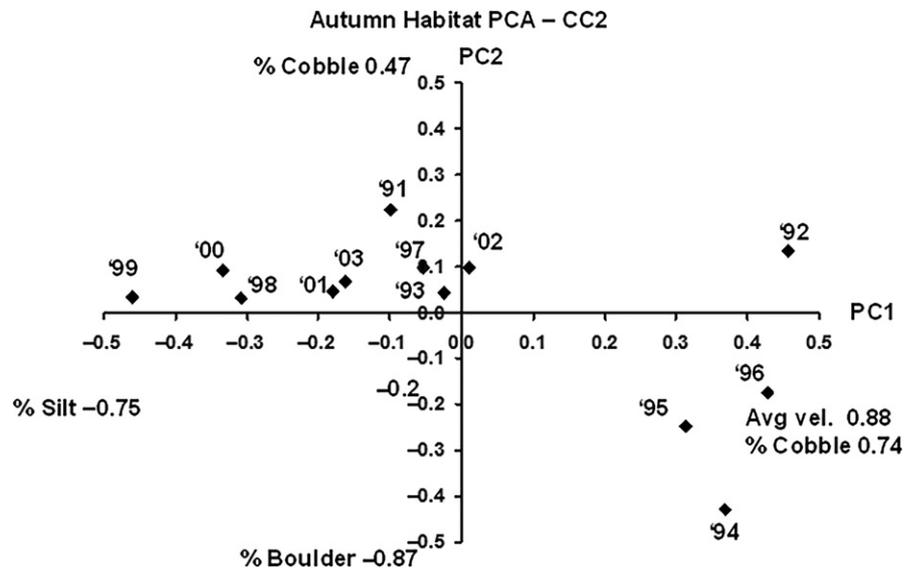
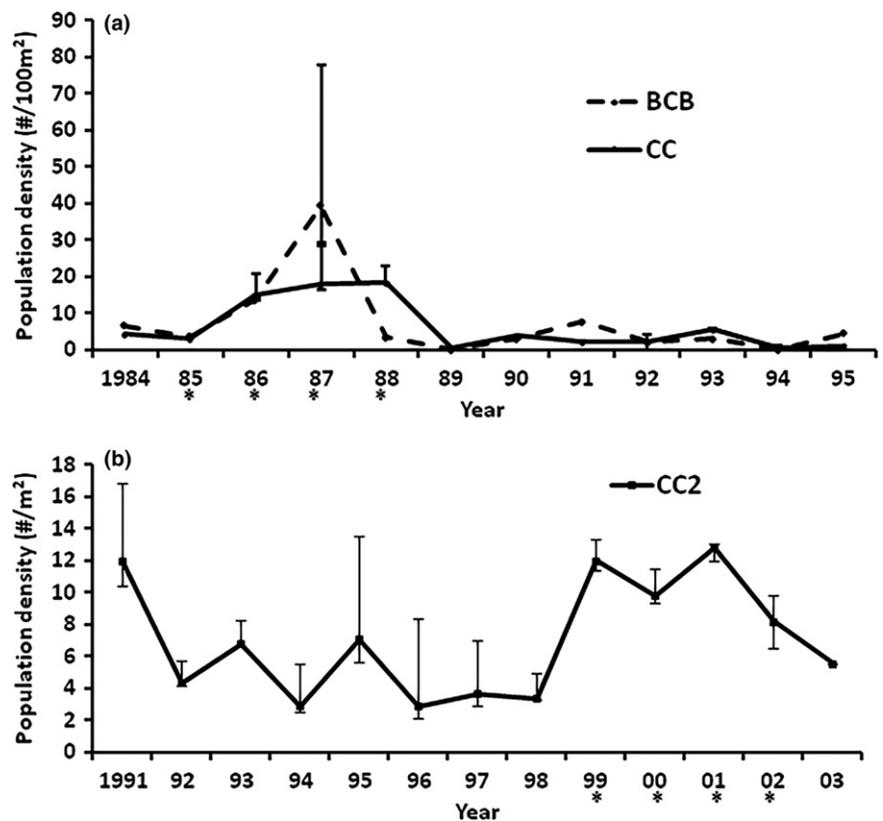Fig. 4 Habitat variability during autumn in CC2. Only variables with loadings >0.40 are reported.

Fig. 5 Autumn density estimates (95% CI) for rosyside dace in BCB, CC and CC2. (a) The dashed line represents data for BCB and the solid line for CC. (b) Data for CC2, note the differences in x and y axes. Asterisks represent drought years.

density dependence. Autumn samples displayed stronger density dependence than spring data, and simple negative density dependence or simple delayed negative density dependence were the models with the highest Akaike coefficients in all three sites during that season (W_i values ranging from 0.44 to 0.88, Table 3). Models

representing negative density-independent effects were interpretable in both CC and CC2 but were 2–7.8 times less likely given the data, than the best density-dependent model (Table 3), and a single case of positive delayed density dependence was observed in CC2 in autumn. The confidence intervals of several models

overlapped zero; hence these results must be interpreted with greater caution (Table 3). Results for spring samples were less clear than those for autumn samples, likely because dace were more strongly affected by winter mortality and high flows than dace during autumn.

Table 1 Test for differences between drought and non-drought samples for rosyside dace. *T*-tests were one-tailed for standard length and mass, with the null being one of equivalence and the alternative that dace were smaller during the drought. Density estimates for BCB and CC were # dace 100 m^{-2} and the values for CC2 # dace m^{-2}. The *t*-test for differences in density were two-tailed. For BCB and CC, the drought lasted from 1985–1988, for CC2 from 1999–2002. Samples are for the population as a whole.

Variable	Season	Site	Non-drought mean	Drought mean
Density	Autumn	CC	4.3	20.5*
		BCB	4.6	19.3**
		CC2	41.9	76.5
	Spring	CC	3.3	9.7***
		BCB	3.5	4.0
		CC2	14.9	32.5*
Standard length	Autumn	CC	61.4	53.5****
	Autumn	BCB	62.4	52.3****
	Autumn	CC2	63.0	60.2****
	Spr	CC	63.6	60.6
	Spr	BCB	61.8	59.8
	Spr	CC2	63.7	62.7
Mass (g)	Autumn	CC	3.95	2.58***
	Autumn	BCB	4.01	2.55***
	Autumn	CC2	4.45	3.56***
	Spring	CC	4.93	4.41
	Spring	BCB	4.70	4.17
	Spring	CC2	5.10	4.82

Non-significant results have no asterisks and significance denoted by *$P < 0.1$, **$P < 0.05$, ***$P < 0.01$, ****$P < 0.0001$.

Interpretable models for spring data contained a greater number of parameters with confidence intervals overlapping zero (seven of nine), resulting in a lower level of confidence in their explanatory power (Table 3). Negative density-independent models (flow variation) were the models with the greatest explanatory power in BCB and CC2 with W_i values of 0.79 and 0.62 respectively. Simple delayed negative density dependence had the greatest explanatory power in CC with a W_i value of 0.70. All interpretable models for CC had parameter confidence intervals that overlapped zero apart from simple delayed negative density dependence, and all were at least 5.8 times less likely to be true, given the data, than the best model.

Growth data

Results for growth data were similar to those for per-capita rate of increase and confirm the importance of density dependence to individual growth (e.g. Fig. 8). In autumn, simple negative delayed density dependence was the model that best explained patterns in growth data in two of three sites, with W_i values ranging from 0.40 to 0.75 (Table 3), but parameter confidence intervals in both cases included zero. Simple negative density dependence was the best model for CC with a W_i of 0.83 and a parameter confidence interval that did not overlap zero. In both BCB and CC2 simple negative density dependence was the second best interpretable model with a likelihood, given the data, of 3.8 (BCB) and 1.1 (CC2) times less than the best model. Confidence intervals for these parameters did not overlap zero. Interpre-
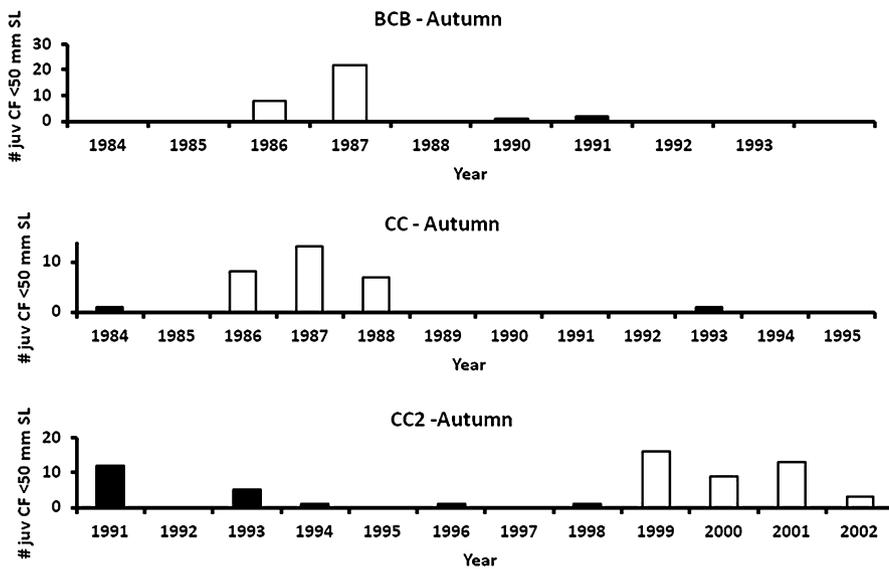

Fig. 6 Abundance estimates of juvenile rosyside dace (<50 mm, SL) in BCB, CC and CC2. Data from non-drought years depicted with solid bars and drought data with open bars.

Table 2 Coefficient of variation estimates for mean annual autumn densities of rosyside dace in BCB, CC and CC2, presented for early and late annual samples in the time series, as well as for drought and non-drought periods.

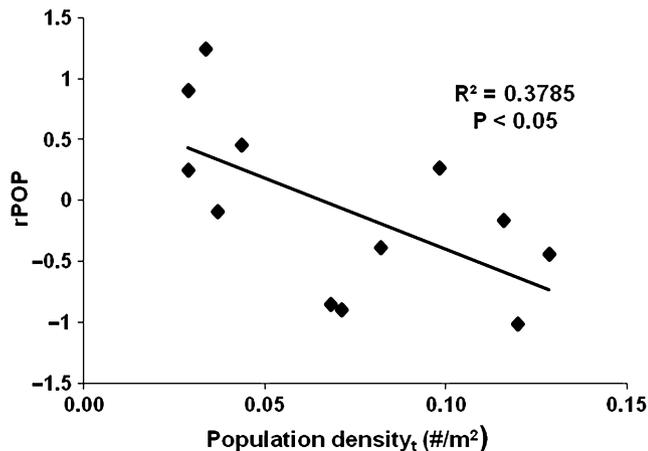|	All Years	Early Years 1984–1989	Late Years 1990–1995	Drought	Non-Drought
BCB	1.48	1.31	0.86	1.13	0.81
CC	1.08	0.82	0.71	0.53	0.72
		1991–1997	1998–2003		
CC2	0.52	0.58	0.43	0.20	0.54

Fig. 7 An example of a regression of per-capita rate of increase vs. density for rosyside dace (Autumn CC2).

tation of results for growth data during spring were less clear with four of five interpretable models having parameter estimates that overlapped zero. The sole model whose confidence interval did not overlap zero was simple density dependence in CC, which also was 2.3 times less likely to be true given the data than simple delayed density dependence. In BCB and CC2, models with positive density dependence were interpretable which suggests that growth was positively affected by environmental conditions that also increased survivorship. Only two of five interpretable models included negative density-dependent effects. Results for spring growth data yield a lower level of confidence; however, because the majority of models had parameter estimates that overlapped zero.

Discussion

We have shown via long-term descriptive and experimental studies that the fish assemblage in the Coweeta catchment is organised primarily via stochastic environmental processes, primarily variation in flow

(Grossman *et al.*, 1998, 2010a; and references therein). Nonetheless, a simple, and relatively old explanation for the maintenance of diversity in such systems (Grossman *et al.*, 1982), is that strong intraspecific competition (i.e. density dependence, Grossman *et al.*, 2010a; Comita et al., 2010; McPeek, 2012) maintains species abundances at levels below which interspecific competition occurs. Our analysis of population data for Rosyside dace, the second most abundant assemblage member in the Coweeta catchment (Grossman *et al.*, 2010a) supports this hypothesis, because this species displays strong evidence of density-dependent population regulation, although weaker negative and positive density-independent effects also were observed. There is no doubt that populations within most assemblages likely are affected by both types of processes, although at times, one may be dominant (Grossman *et al.*, 2006, 2012).

The mechanism by which rosyside dace populations are regulated by density dependence most likely is intraspecific competition for profitable foraging positions via intraspecific aggression (Freeman & Grossman, 1992b; Rincon & Grossman, 2001; Wagner & Grossman, 2013). Although many dace are non-aggressive, others display intraspecific aggression, excluding conspecifics from favourable foraging spots with higher food availability, and thus obtaining higher foraging rates (Freeman & Grossman, 1992b; Rincon & Grossman, 2001; Hazelton & Grossman, 2009). We have observed this mechanism in both field and laboratory stream studies, although the phenomenon was most apparent in laboratory studies (Freeman & Grossman, 1992b; Rincon & Grossman, 2001; Hazelton & Grossman, 2009; Wagner & Grossman, 2013).

Rosyside dace populations displayed a strong positive relationship between drought and recruitment, but the causal mechanism driving this correlation remains uncertain, given our data. It is possible that low flows resulted in either increased survival or increased immigration of rosyside dace into study sites; although Hill & Grossman (1987) used mark-recapture analysis to show that many rosyside dace had home ranges smaller than the 30 m study sites. Hill & Grossman (1987) also noted that rosyside dace residing in pools or riffles without current velocity refuges (e.g. undercut banks or submerged brush) appeared to be displaced downstream by high flow events. If immigration occurred in our study sites, it must have come from downstream because the sites are at the upstream limit of rosyside dace distribution in the Coweeta catchment (personal observation). Despite potentially higher survivorship or immigration, drought may have produced stressful physiological conditions for YOY dace, slowing their growth, in compar-

Table 3 Model selection analysis for per-capita rate of increase and growth data for rosyside dace in the Coweeta catchment. Variables are response variable (per capita rate of change or mean SL), site, the candidate model, Akaike's Information Criterion for small samples (AICc), delta AIC (ΔAICc), Akaike weight (w_i) and the explanatory power (in parentheses) of a competing model when compared to the model with the highest w_i. Candidate models whose parameter 85% confidence intervals overlap zero are denoted with an asterisk.

Response Variable Site	Candidate Model	AICc	ΔAICc	w_i
Per capita rate of change				
Autumn				
Population BCB	Simple Delayed Density Dependence, rpop $= -f(\text{dpop}_{t-1})$	75.16	0.00	0.88
CC	Simple Density Dependence, rpop $= -f(\text{dpop})$	66.18	0.00	0.44
	*Simple Delayed Density Dependence, rpop $= -f(\text{dpop}_{t-1})$	67.15	1.07	0.26 (1.7 X)
	Simple Negative Density Independence (Flow), rpop $= -f(\text{FPC1}_t)$	67.54	1.36	0.22 (2.0 X)
	*Simple Delayed Positive Density Independence (Flow), rpop $= f(\text{FPC1}_{t-1})$	69.37	3.19	0.09 (4.9 X)
CC2	Simple Density Dependence, rpop $= -f(\text{dpop})$	49.36	0.00	0.54
	*Simple Delayed Positive Density Dependence, rpop $= f(\text{dpop}_{t-1})$	51.73	2.37	0.17 (3.3 X)
	Simple Density Dependence & Simple Negative Density Independence (Flow), rpop $= -f(\text{dpop}) - f(\text{FPC1}_t)$	52.04	2.68	0.14 (3.8 X)
	Simple Negative Density Independence (Flow), rpop $= -f(\text{FPC1}_t)$	53.48	4.12	0.07 (7.8 X)
Spring				
Population BCB	Simple Negative Density Independence (Flow), rpop$=-f(\text{FPC1}_t)$	63.97	0.00	0.79
	*Simple Delayed Density Dependence, rpop $= -f(\text{dpop}_{t-1})$	67.78	3.81	0.12 (6.7 X)
CC	*Simple Delayed Density Dependence, rpop $= -f(\text{dpop}_{t-1})$	64.21	0.00	0.70
	*Simple Density Dependence, rpop $= -f(\text{dpop})$	67.74	3.53	0.12 (5.8 X)
	*Simple Delayed Negative Density Independence (Flow), rpop $= -f(\text{FPC1}_{t-1})$	68.33	4.12	0.09 (7.8 X)
	*Simple Positive Density Independence (flow), rpop $= f(\text{FPC1}_t)$	68.36	4.15	0.09 (8.0 X)
CC2	Simple Negative Density Independence (flow), rpop $= -f(\text{FPC1}_t)$	63.44	0.00	0.62
	*Simple Delayed Density Dependence, rpop $= -f(\text{dpop}_{t-1})$	65.14	1.70	0.26 (2.3 X)
	*Simple Density Dependence, rpop $= -f(\text{dpop})$	67.60	4.16	0.08 (8.0 X)
Growth (mean standard length)				
Autumn				
Population BCB	*Simple Delayed Density Dependence, pop SL $= -f(\text{dpop}_{t-1})$	84.93	0.00	0.75
	Simple Density Dependence, pop SL $= -f(\text{dpop}_t)$	87.62	2.69	0.19 (3.8 X)
CC	Simple Density Dependence, pop SL $= -f(\text{dpop})$	86.91	0.00	0.83
	*Simple Delayed Density Dependence, pop SL $= -f(\text{dpop}_{t-1})$	90.89	3.98	0.11 (7.3 X)
CC2	*Simple Delayed Density Dependence, pop SL $= -f(\text{dpop}_{t-1})$	96.35	0.00	0.43
	Simple Density Dependence, pop SL $= -f(\text{dpop})$	96.50	0.14	0.40 (1.1 X)
	Simple Positive Density Independence (Flow), pop SL $= f(\text{FPC1}_t)$	98.45	2.10	0.15 (2.9 X)
Spring				
Population BCB	*Simple Delayed Positive Density Dependence, pop SL $= f(\text{dpop}_{t-1})$	80.16	0.00	0.89
CC	*Simple Delayed Density Dependence, pop SL $= -f(\text{dpop}_{t-1})$	88.28	0.00	0.64
	Simple Density Dependence, pop SL $= -f(\text{dpop})$	89.96	1.68	0.28 (2.3 X)
	*Simple Positive Density Independence (Flow), pop SL $= f(\text{FPC1}_t)$	92.46	4.18	0.08 (8.1 X)
CC2	*Simple Delayed Positive Density Dependence, pop SL $= f(\text{dpop}_{t-1})$	95.56	0.00	0.93

ison to non-drought years. As a consequence, the increase in YOY during drought years could have been produced by an increased ability to detect these smaller fish, because they would not have grown sufficiently to reach a size at which they were indistinguishable from 1+ fish (i.e. >50 mm SL). We can distinguish between the 'stress' vs. survivorship/immigration hypotheses; however, by examining density estimates for rosyside dace during drought and non-drought periods versus the concomitant decreases in mean wetted site areas. If the increases in density are greater than the proportional decrease in wetted area, then either increased survivorship of YOY or increased immigration are occurring. The decrease in wetted area in all sites ranged from 10–

21 %; however, the increases in abundance were much larger, in some cases, orders of magnitude (Table 1), so it is unlikely that the increase in YOY density in drought years was a function of decreased growth due to physiological stress.

Drought effects on rosyside dace also were reflected in the interpretable models depicting both negative and positive relationships between flow and the per-capita rate of increase observed in all three sites. However, density dependence had a stronger impact on these populations than flow effects. Finally, the hypothesis that species are maintained within this stochastic assemblage by strong intraspecific density dependence (intraspecific competition) that maintains populations below levels at

which interspecific competition occurs, is further supported by long-term population studies of the numerically dominant assemblage member the mottled sculpin, *Cottus bairdi* (Grossman *et al.*, 2006; Petty & Grossman 2010), and the dominant headwater species southern brook trout, *Salvelinus fontinalis* (Grossman *et al.*, 2010b), both of which exhibit strong density-dependent population regulation.

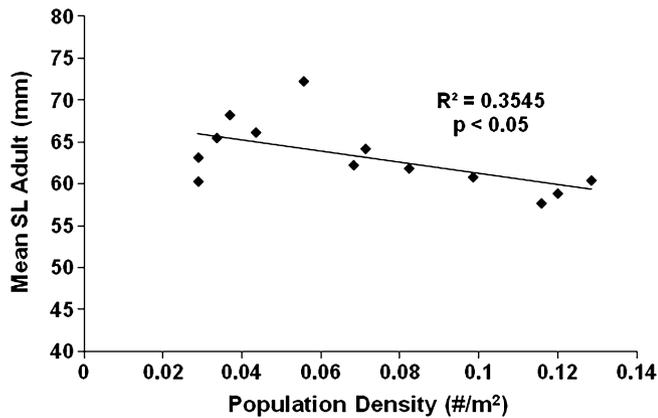Our results should be robust, given that they were obtained from three sites (two different site-sizes, two

Fig. 8 An example of a regression of growth (mean annual SL) vs. density rosyside dace (Autumn CC2).

different but somewhat overlapping time periods) over a 20-year period. Consequently, they should serve as a good baseline against which to examine changes correlated with GCC: especially increased environmental variability. If, as predicted, GCC results in increased variability in flows, then we would expect both extreme high and low flow events to increase in frequency. Increased high flows will lead to reductions in recruitment and ultimately density, with reduced intraspecific competition and increased body size (Tables 1, 2, Fig. 9). Increases in years with prolonged low flows will produce increased recruitment and density, whereas average flow years will yield intermediate results. If GCC does produce increases in the frequencies of years with extreme events, this likely will reduce the effects of density dependence within these populations. A reduction in density-dependent forces could destabilise rosyside dace populations, by reducing their ability to respond in a compensatory manner. Population destabilisation would be especially likely after a series of high water years, when rosyside dace densities are driven down, probably via flow-induced mortality. Because of a lack of important interspecific interactions within this assemblage (Grossman *et al.*, 2010a), we have focused on the direct effects of GCC on rosyside dace. These effects are manifested mainly through responses to varying flow
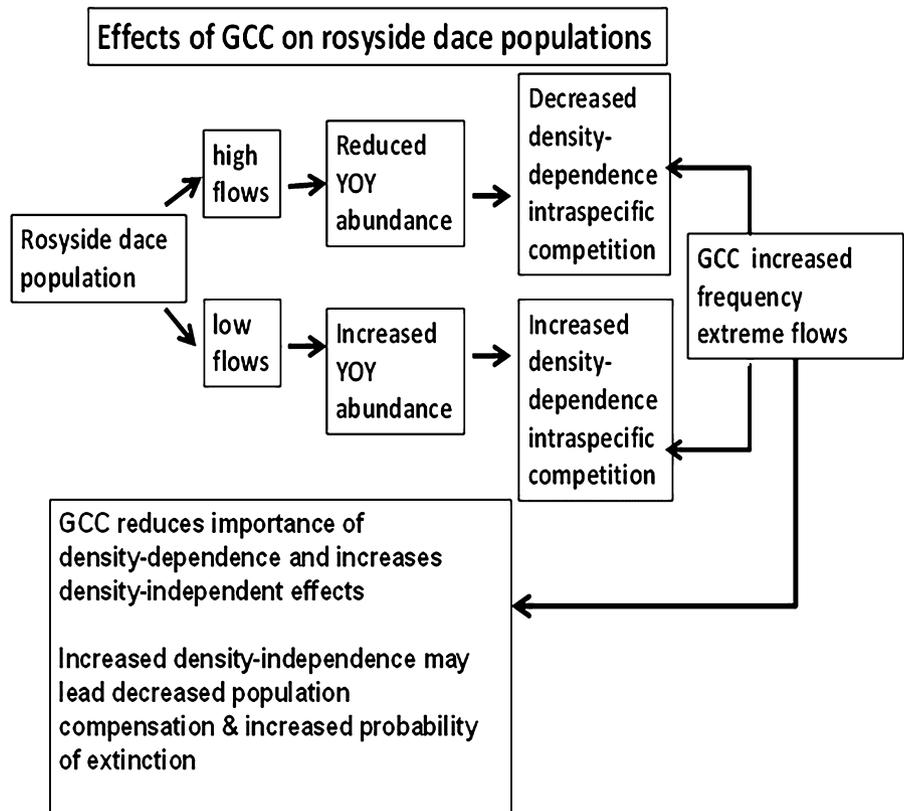

Fig. 9 A conceptual model of how global climate change will affect the rosyside dace population in the Coweeta catchment.

regimes rather than changes in temperature (Grossman *et al.*, 2006). Nonetheless, directional GCC (e.g. shifts to high flow regimes or increased stream temperatures) could result in ecosystem-level changes resulting in increased importance of interspecific interactions in this system, as has been shown by Jackson & Mandrak (2002) for Canadian cyprinids occupying lakes. Directional GCC might shift the trophic base of this assemblage via its effects on both within stream and terrestrial primary producers. In addition, increased temperatures might result in a contraction of the range of rosyside dace.

Density dependence has been documented in many fish populations (Hixon, Pacala & Sandin, 2002; Minto C., Myers R.A. & Blanchard W. 2008), although most of these studies focus on species of economic importance such as marine or sport fisheries. Of particular note are the long-term studies of brown trout (*Salmo trutta*) by both Elliott (1994) and Lobon-Cervia (2007, 2012, 2014), which found strong impacts of both density-dependent and density-independent factors on this species, although they operated on different life-history stages. Our studies of Coweeta fish show strong density dependence in the most abundant members of both the water-column (rosyside dace) and benthic guilds (mottled sculpin), although both species also displayed density-independent impacts on YOY (herein and Grossman *et al.*, 2006). Density dependence has been found in a variety of other freshwater fish, including species from multiple continents (Grenouillet *et al.*, 2001; Davey *et al.*, 2006; Jellyman & McIntosh, 2010), and may represent a general pattern of population regulation in this taxon, although evidence from harsh climates also demonstrates that density independence, especially in the form of flow variation may significantly affect minnow populations (Nunn *et al.*, 2003, 2007; Durham & Wilde, 2009a,b; Wilde & Durham, 2008). It is also possible that water temperatures play a role in population variation in these species because flow variation and water temperature likely covary in most systems. Nonetheless, there are few long-term, mechanistic population studies of cyprinids or other non-game fish, although these species comprise the majority of fish world-wide.

In conclusion, our findings provide a long-term benchmark against which future studies on this abundant minnow can be evaluated. As GCC increases, we predict that rosyside dace will show a variety of potential effects, including increased abundance coupled with reduced growth in low water years, and the opposite characteristics in high water years. If directional GCC occurs in the form of increased high water years, we predict that rosyside dace populations will become less stable because of a reduced capacity to display compensatory demographic responses. Our findings demonstrate the need for long-term research and hopefully will aid in conservation strategies for temperate fish at the southern edges of their distributional ranges. Such species are likely to be the ones most affected by GCC.

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Appendix 1: Variable loadings for flow PCA figure axes

Fig. 2a CC2 – spring

1. PC1 – May_{t-1} to May_t mean flow 0.94, May_{t-1} to Sep_{t-1} # high flows 0.88, May_{t-1} to May_t # high flows 0.91, May_{t-1} to Sep_{t-1} mean min flow 0.84, May_{t-1} to Sep_{t-1} min flow 0.76, Oct_{t-1} to May_t # high flows 0.74, May_{t-1} to May_t max flow 0.63, May_{t-1} to Sep_{t-1} max flow 0.64, Oct_{t-1} to May_t max flow 0.63.

2. PC2 – Oct_{t-1} to May_t max flow 0.67, May_{t-1} to May_t max flow 0.67, May_{t-1} to Sep_{t-1} max flow -0.61, Oct_{t-1} to May_t # high flows 0.42, May_{t-1} to Sep_{t-1} min flow −0.40, May_{t-1} to Sep_{t-1} high flows −0.40

Fig. 2b CC2 – autumn

1. PC1 – $Sept_{t-1}$ to $Sept_t$ # high flows 0.90, $Sept_{t-1}$ to $Sept_t$ mean flow 0.89, May_t to $Sept_t$ mean min flow

0.83, Oct_{t-1} to May_t # high flows 0.80, May_t to $Sept_t$ min flow 0.75, $Sept_{t-1}$ to $Sept_t$ max flow 0.74, May_t to $Sept_t$ # high flows 0.71, May_t to $Sept_t$ max flow 0.66, Oct_{t-1} to May_t max flow 0.60.

2. PC2 – Oct_{t-1} to May_t # high flows 0.80, Oct_{t-1} to May_t max flow 0.68, $Sept_{t-1}$ to $Sept_t$ max flow 0.45, May_t to $Sept_t$ # high flows −0.67, May_t to $Sept_t$ mean min flow −0.51 May_t to $Sept_t$ max flow −0.50, May_t to $Sept_t$ min flow −0.49

Fig. 3a BCB & CC spring

1. PC1 – May_{t-1} to May_t mean flow 0.97, May_{t--1} to May_t # high flows 0.92, May_{t-1} to Sep_{t-1} # high flows 0.91, Oct_{t-1} to May_t # high flows 0.84, May_{t-1} to Sep_{t-1} mean min flow 0.81, May_{t-1} to May_t max flow 0.81, May_{t-1} to Sep_{t-1} max flow 0.81, Oct_{t-1} to May_t max flow 0.78, May_{t-1} to Sep_{t-1} min flow 0.68.

2. PC2 – Oct_{t-1} to May_t max flow 0.58, May_{t-1} to May_t max flow 0.48, Oct_{t-1} to May_t # high flows 0.41, May_{t-1} to Sep_{t-1} max flow -0.69, May_{t-1} to Sep_{t-1} mean min flow −0.57,

Fig. 3b BCB & CC autumn

1. PC1– $Sept_{t-1}$ to $Sept_t$ # high flows 0.96, $Sept_{t-1}$ to $Sept_t$ mean flow 0.91, $Sept_{t-1}$ to $Sept_t$ max flow 0.85, Oct_{t-1} to May_t # high flows 0.85, May_t to $Sept_t$ mean min flow 0.80, May_t to $Sept_t$ min flow 0.75, May_t to $Sept_t$ # high flows 0.67, May_t to $Sept_t$ max flow 0.67, Oct_{t-1} to May_t max flow 0.51.

2. PC2 – Oct_{t-1} to May_t max flow 0.83, May_t to $Sept_t$ # high flows −0.66, May_t to $Sept_t$ max flow −0.59, May_t to $Sept_t$ mean min flow −0.56, May_t to $Sept_{t-1}$ min flow −0.53, Oct_{t-1} to May_t # high flows 0.50.