Biotic and abiotic regulation of a low-density stream-dwelling brown trout (*Salmo trutta* L.) population: effects on juvenile survival and growth

Alexandre Richard[1,2], Franck Cattanéo[1], Jean-François Rubin[1,3]

[1]hepia, Geneva Technology, Architecture and Landscape, University of Applied Sciences Western Switzerland, Jussy (GE), Switzerland
[2]UMR 0042 Carrtel, INRA, Thonon, France
[3]Maison de la Rivière, Tolochenaz, Switzerland

Abstract – The effects of biotic (density-dependent) and environmental (flow and temperature) factors on the apparent survival, mean length and size variation of a low-density brown trout population in the juvenile stage, that is, from their first summer (0+) to the end of the second year (1+), were determined. Apparent survival was negatively related to the age class density during the three periods (first summer, first winter and second summer). A significant interaction between the mean flow and 0+ density highlighted a gradient towards strong density dependence acting on fish loss (i.e., mortality or migration) with decreasing summer flow. Conversely, no density dependence was reported at higher mean flows. The mean length was determined by density-dependent and density-independent (temperature and flow) factors throughout the study period. The negative relationship between fish length and intracohort density was highly significant during the three periods. The yearling (1+) density was negatively related to 0+ fish length measured after the first summer, suggesting intercohort effects. A positive effect of temperature on fish length was observed. Mean length after the summer seasons (0+ and 1+ fish) was also positively related to mean flow. Fish size variation around the mean measured with the coefficient of variation (CV) increased with increasing 0+ densities, both at the end of the first summer and the first winter. Results suggested that density-dependent and density-independent factors acted jointly on apparent survival and growth with a predominance of biotic processes. We discussed the potential implications of density-dependent regulations on growth and survival for population resilience after catastrophic events.

Key words: Density dependence; abiotic factors; juvenile; *Salmo trutta*; survival; growth

Introduction

Density-dependent demographic processes contribute to the regulation of natural populations of a wide range of invertebrate, vertebrate and plant species (Brook & Bradshaw 2006). Stream-dwelling salmonids are relevant biological models to study such processes because they inhabit a variety of streams, where they compete for territory *via* interference and/or for food *via* exploitative competition (Keeley 2001). Density-dependent processes in wild salmonid populations have been extensively studied (e.g., Grant & Kramer 1990; Crisp 1993; Elliott 1994) and may be expressed either by mortality, dispersal or an impaired growth rate. Whether one of these modes of regulation prevails over the others primarily depends on the ontogenetic stage and population density.

Density-dependent effects on individual survival have been reported at early life stages from emergence to 30–70 days postemergence when young-of-the-year (YOY) start to compete for food and

territory (e.g., Elliott 1994; Jonsson et al. 1998; Einum & Nislow 2005). Thereafter, as fish grow and increase their fat reserves, survival remains relatively constant and density-independent (Elliott 1985), at least during the first year. Meanwhile, YOY dispersal abilities increase with size, and some fish (presumably in poorer condition and/or hierarchically subordinate individuals) tend to move from high density to low-density patches (Crisp 1993; Einum et al. 2006).

A high fish density may also involve *per capita* food limitation. This limitation results in a decrease in growth rate (commonly expressed by mean weight, length, or instantaneous growth rate) that is generally observed at the end of the growing season of 0+ fish (Grant & Imre 2005). The relationship between growth and density has been investigated both in well-designed experimental studies in artificial channels (Jenkins et al. 1999; Keeley 2001) and *in situ*, by means of medium- to long-term (i.e., from eight to 14 cohorts) monitoring of natural populations (Atlantic salmon *Salmo salar* L., Imre et al. 2005, 2010; brown trout, Lobón-Cerviá 2005; marble trout *Salmo marmoratus* Cuvier, 1829, Vincenzi et al. 2007). Most often, growth–density relationships were best fitted by negative power curves; this implies that density dependence is best observed at low densities, even though Lobon-Cervia (2007a) concluded that this process operated both at high and low densities. In a meta-analysis of 16 different studies on six species of resident salmonids, Grant & Imre (2005) presented evidence for a density-dependent growth in 75% of the referred populations. The inability to relate growth to density could be either due to a narrow density range or to the observed high mean density for which density-dependent effects become negligible (Jenkins et al. 1999; Lobon-Cervia 2007a).

According to the site profitability hypothesis, as density increases, the number of slow-growing fish also increases because the best feeding sites are already occupied, thus relegating additional individuals to lower quality sites (Newman 1993). Consequently, a higher coefficient of variation in size (CV) should be observed with increasing density. The size variation around the mean has been positively related to the YOY cohort strength in brown trout populations (Newman 1993; Jenkins et al. 1999; Nordwall et al. 2001; Lobón-Cerviá 2010). Conversely, Imre et al. (2010) did not observe a significant effect of Atlantic salmon density on size variation expressed by the standard deviation. Mean size and size variation are site-specific and depend on several factors (e.g., temperature, flow, food abundance, interspecific competition), other than intraspecific relationships only. Therefore, multiple years of monitoring data on multiple sites displaying a large span of densities may help elucidate the biotic and abiotic

factors that govern the observed inter-annual growth variations.

The relative importance of abiotic factors on juvenile salmonid survival and growth, such as temperature (e.g., Elliott & Elliott 1995; Jensen et al. 2000; Logez & Pont 2011), flow (e.g., Cattanéo et al. 2002; Unfer et al. 2011; Nislow & Armstrong 2012), habitat availability (Armstrong et al. 2003) or a combination of these factors (Clews et al. 2010), has been intensively investigated. Several studies focused on the joint effects of fish density and temperature (Crozier et al. 2010; Bal et al. 2011; Parra et al. 2012; Bærum et al. 2013) or densities and flow (Lobón-Cerviá 2004; Lobon-Cervia 2007b; Teichert et al. 2010; Cunjak et al. 2013), but only a few have addressed the combined effects of cohort densities (intra- and intercohort relationships) and environmental features (temperature and flow; but see Carline 2006; Vøllestad & Olsen 2008; Grossman et al. 2010, 2012).

The concurrent analysis of biotic and environmental factors (including interactions) is crucial for improving our understanding of the processes influencing population changes in space and time (Milner et al. 2003). More precisely, the juvenile stage (i.e., first two years of life) is of major interest for population dynamics, because it corresponds to highly variable cohort densities and to a potential population bottleneck. While long-term series are required to improve our knowledge of regulatory processes (biotic or abiotic), uncertainties in population estimates should also be considered to improve the robustness of models (Milner et al. 2003).

In this study, we aimed to unravel the factors governing the dynamics of a resident brown trout population during the juvenile stage. Based on 12 years of monitoring in 11 river reaches, we evaluated the respective effects of density-dependent and density-independent (temperature and flow) processes on 'apparent survival' (recapture of live individuals in the capture site), mean size and size distribution of juvenile brown trout from their first summer (YOY, 0+) until the end of their second year (yearlings, 1+ fish). We tested with simulation analysis whether the observation of density dependence on apparent survival was robust to sampling error.

Materials and methods

Study reaches and survey

The Boiron River is a 13.4-km-long tributary of the north edge of Lake Geneva in Switzerland (46°29′29″N and 6°28′47″W at the outlet). The river originates in the foothills of the Jura Mountains from the drainage of the old marshes, at an altitude ranging

between 665 and 372 msl. The interannual mean flow (i.e., mean across years of annual mean daily flows) is 0.27 $m^3 \cdot s^{-1}$. Most of the watershed (catchment area = 31.6 km^2) is covered by cultivated fields, mainly cereals, meadows and vineyards.

Only three fish taxa thrive in the Boiron: brown trout, European bullhead (*Cottus gobio* L.) and minnow (*Phoxinus phoxinus* L.). Some indigenous crayfish (*Austropotamobius pallipes* Lereboullet 1858) have colonised the upper reaches. At the river outlet, the species richness locally increases up to 10 species due to the presence of Lake Geneva. Although barriers to migration have been progressively restored and equipped with fish passes, an impassable waterfall (Fig. 1) still impedes anadromous brown trout migration from the lake. The population freely fluctuates, as no supplemental stocking has been carried out in the last 12 years. Age at maturity is generally 2 years for males and 3 years for females; lifespan rarely exceeds 5 years. Angling is allowed, but brown trout harvesting has been moderate as reported by angler catch records (approx. 200 captures/year throughout the river).

Nine reaches (BO1 to BO9 from up to downstream) were studied along the mainstem (Fig. 1) and two in the major tributaries: Lécherres (LE1) and Boironnet (BT1). Each studied reach was representative of a homogeneous river section regarding mean slope and mesohabitat conditions (Malavoi & Souchon 2002). Reaches BO1 to BO7 were located in the river section harbouring resident trout only. Reaches BO8 and BO9 were located downstream of the impassable waterfall, where both resident and migratory individuals may spawn. Reach lengths ranged between 47 and 91 m (mean ± SD length = 65 ± 12 m), and the wetted width at the median interannual flow ranged between 1.0 and 4.3 m (mean ± SD width = 2.7 ± 1.2 m). The length/mean width ratio exceeded 13 in all reaches and included at least two riffle-pool sequences (Keller & Melhorn 1978). Habitat measurements were performed in the spring and autumn 2009 in eight of 11 reaches (all except BO3, LE1 and BT1) following the simplified instream habitat model described by Lamouroux & Capra (2002). Output curves linking habitat value (HV, ranging between 0 and 1) and flow for juvenile brown trout (0+ and 1+) exhibited similar shapes and similar HV at median flow (Q50) between reaches (range = 0.44–0.55; mean = 0.50; unpublished data). We therefore concluded that habitat
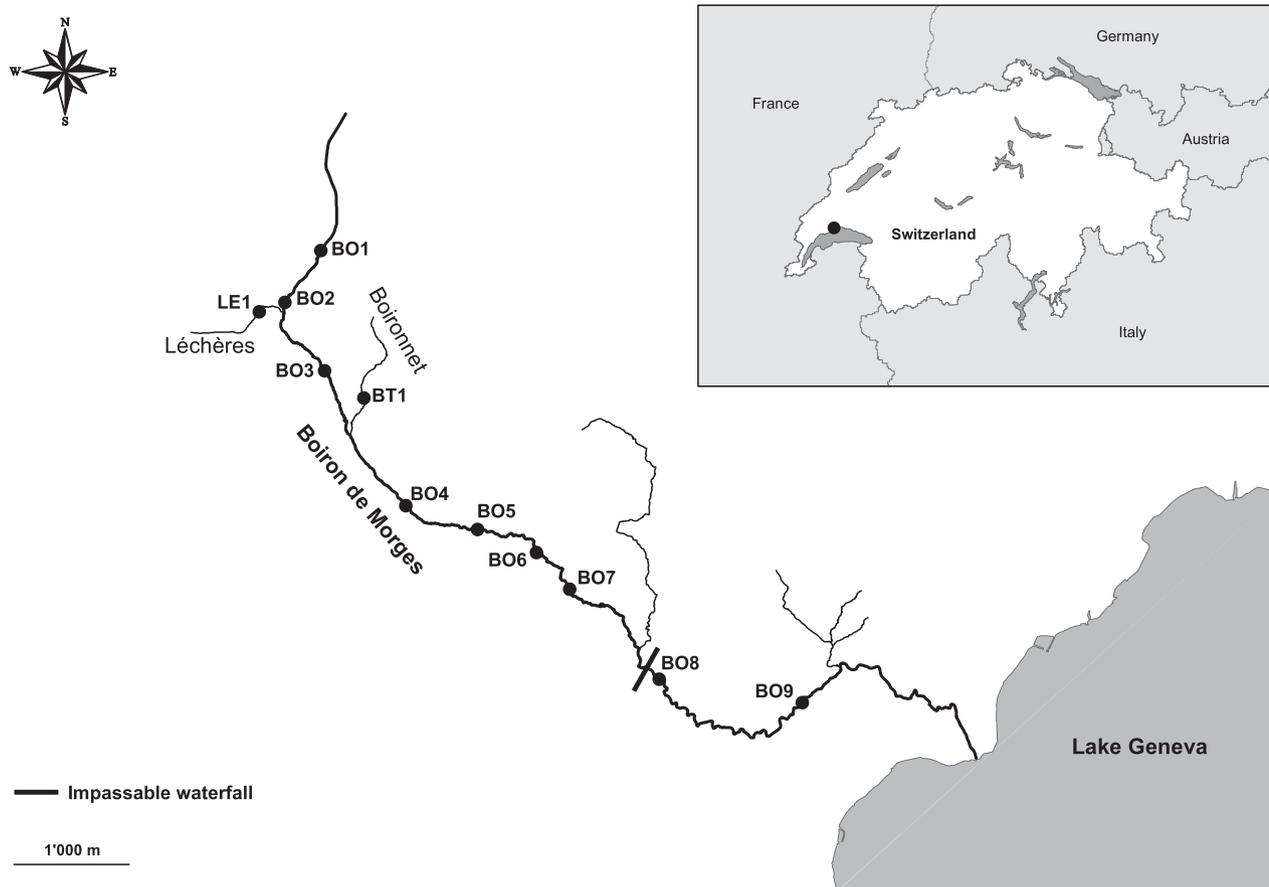
Fig. 1. Location of study reaches.

availability for juveniles little differed between reaches and decided not to include this variable in the analyses.

Brown trout monitoring started in November 2001. All 11 reaches were electrofished twice a year (July and November) until November 2012 following a two-run-removal method. As a severe organic pollution occurred in August 2011 in the downstream section, the data from four reaches (BO6 to BO9) collected after July 2011 were subsequently removed from analyses. Therefore, a total of 121 year-classes were monitored. Captured fish were first anaesthetised with 10% clove oil (3 ml in 10 l of water), then dissolved in ethanol at a ratio of 1:10, measured (total length in mm) and weighed (precision = $\pm$ 0.1 g; from July 2008). Scales were collected from a subsample of fish ($N = 5276$ fish from 15,138 captures). By combining scalimetry and length-frequency histogram analyses, each individual was assigned to one of the following age classes: young-of-the-year (0+), juveniles (1+) or adults (>1+). Trout densities (individuals per 100 m^2 [95% CI]) were assessed per reach and age class following the Carle & Strub (1978) method. The following three ontogenetic stages were considered when analysing regulatory processes: first summer (0+ from July to November in year n), first winter (0+ from November in year n to July in year $n + 1$) and second summer (1+ from July to November in year $n + 1$). Because of the interval between sampling occasions (4 summer months and 8 winter months), the winter period also covered part of the previous autumn and the following spring.

Temperature and flow data

Environmental data were analysed over two periods corresponding to the above-defined stages: from 1st July to 1st November of year n (summer period, for both 0+ and 1+) and from 1st November of year $(n-1)$ to 1st July of year n (winter period). Water temperature records were initiated in November 2004 at two locations (reaches LE1 and BO2). In 2008, all 11 reaches were equipped with a temperature logger (HOBO Water Temp Pro v2 Data Logger, Onset), except BO6 and BO7, which shared the same sensor. Water temperature was recorded every 10 min with a precision of 0.2 °C at 25 °C. Missing data (2001–2008) were back-calculated for each study reach from daily mean air temperatures collected at the nearby MeteoSwiss (Federal Office of Meteorology and Climatology) station of Changins (long: 6°14′; lat: 46°24′; 455 m.a.s.l.) using ordinary least-square linear regressions. All correlation coefficients between mean daily air and water temperatures were high (mean $R^2 = 0.91$, range = 0.87–0.94), although a lower value was obtained on the reach LE1 ($R^2 = 0.71$), which is located in a secondary spring. Nine variables were computed for each reach and each period from the mean daily temperature data: the maximum (Tmax), minimum (Tmin), mean (Tmean), and median temperature (T50), the temperature variance (Tvar), the temperature corresponding to the 90th (T90) and 10th (T10) percentiles, the number of days bellow the interannual T90 ($N < $ T90), and the number of days above the interannual T10 ($N > $ T10).

Flow data

A gauging station located 300 m upstream of the Boiron outlet has been recording flow every 10 min since 2009. During 2001–2009, a nearby gauged river (Morges) displaying a similar watershed area (31.6 km^2 for Boiron; 35.6 km^2 for Morges) and collecting the same rainfall amount was used as a proxy to assess daily mean flow values (B. Cordey, hydrologist, General Directorate for Environment of the Vaud canton, personal communication). Daily mean flows of the two rivers were highly correlated between 2009 and 2012 ($Q_{Boiron} = 1.011 * Q_{Morges}$; $R^2 = 0.976$; $N = 1249$), thus allowing a reliable back-calculation of the flow on the Boiron during 2001–2009. Nine hydrological variables were calculated for each period from daily mean flow data: the maximum (Qmax), minimum (Qmin), mean (Qmean), and median flow (Q50), the flow variance (Qvar), the flow corresponding to the 90th (Q90) and 10th (Q10) percentiles, the number of days below the interannual Q90 ($N < $ Q90), and the number of days above the interannual Q10 ($N > $ Q10).

Statistical analyses

All statistical analyses were performed using R (R Development Core Team. 2012). Normalised principal components (PCA) analyses were implemented separately on flow and temperature variables to synthesise the information on a small number of independent components. Analyses were performed during the summer period and the winter period. Flow and temperature data were first ($\log_e + 1$) transformed to approach normality. Projections of the sample's (year x reach) scores on the two-first PCA axes were used as synthetic explanatory variables (namely, Q_1 and Q_2 for flow; T_1 and T_2 for temperature).

The densities were ($\log_e + 1$) transformed to approach normality. Apparent survivals were calculated as the ($\log_e + 1$) ratios between the final and initial densities for each life stage: first summer (S_{sum0+}), first winter (S_{win0+}) and second summer

(S_{sum1+}). The mean total length (L_{nov0+}, L_{jul1+}, L_{nov1+}) and coefficient of variation (CV_{nov0+}, CV_{jul1+}, CV_{nov1+}) for the length (i.e., the ratio between the standard deviation and arithmetic mean length) were also calculated at the end of each period and were ($log_e + 1$) transformed in order to approach normality. Only samples with >3 fish were analysed. Apparent survival values >150% (which could presumably occur as a result of immigration, in particular under low initial year-class density) were considered as outliers and were removed from survival analyses (Zorn & Nuhfer 2007). Because two reaches (BO8 and BO9) were located in the downstream section accessible to migratory trout, all apparent survival analyses were performed with and without the two reaches. Because the results were unchanged, the two reaches were included in all analyses.

Linear mixed effects models (LMM) were used to test for the respective effects of initial densities per age class (D_{0+}, D_{1+} and $D_{>1+}$), temperature (T_1 and T_2) and flow (Q_1 and Q_2) on each life trait (apparent survival, mean length and coefficient of variation for length). The year and reach were included as random effects in analyses. A top-down strategy was used for model selection (Zuur et al. 2009; Parra et al. 2012). A beyond optimal model (Zuur et al. 2009) was first defined; it included all the main effects and only the main relevant two-way interactions (i.e., between initial densities and environmental variables). The random structure was tested using REML (restricted maximum likelihood) estimation and likelihood-ratio tests; *P*-values were corrected as likelihood ratios follow a $0.5 \times \chi_1^2$ distribution (Zuur et al. 2009). Finally, the fixed structure was searched using the maximum likelihood estimation (ML). As variables were measured on different scales, they were standardised using the *arm* package (Gelman & Su 2013) to facilitate the interpretation of the relative magnitude of the estimates (Grueber et al. 2011). Model selection and averaging were implemented using the Akaike's Information Criterion corrected for small sample size (AICc) with the *MuMIN* package (Barton 2013). A top model set satisfying the criterion ΔAICc < 2 from the best model was selected (Burnham & Anderson 2002). Model averaging was processed on the selected models using the natural average method for coefficient estimates (Burnham & Anderson 2002; Grueber et al. 2011). This method averages the parameter estimates only over models in which the predictor appears and provides 95% confidence intervals and Wald *Z* tests for averaged estimates. The relative importance (Imp) of each parameter was calculated as the sum of the weights of the different models that included this parameter. A relative importance of 1 indicated that the parameter was included in all of the selected models. In case

of significant interactions, the *effect* package (Fox 2003) was used to display the interactive effect.

For analysing the apparent survival, the effect of density estimate uncertainty (due to a capture probability <1) on model robustness was tested using resampling. Resampling (10,000 iterations) was performed by randomly selecting densities (initial and final) within the 95% confidence interval provided by the Carle and Strub method, assuming a uniform distribution within the confidence interval range. Model selection and averaging were reapplied to each data set, and the significance of each variable was tested using Wald *Z* tests.

Results

Temperature

For the summer season, the first two PCA axes explained 85.7% of the total variance (Fig. S1). The first axis (T_1) correlated with the mean and maximum temperatures, while the second axis (T_2) predominantly correlated with the minimum temperature. The interannual average reach positions (barycentres) were mainly distributed along T_1, which accounted for the thermal gradient. For the winter period, the two-first axes explained 73.0% of the variance. T_1 primarily correlated with the maximum temperature and the temperature variance, whereas T_2 correlated with the mean and median temperatures. The reaches were similarly distributed along T_1 as in the summer period.

Flow

During the summer, the first two PCA axes (Q_1 and Q_2) explained 97.6% of the variance (Fig. S2). The first axis (76.6% of the total variance) corresponded to a flow level gradient, where all 9 variables highly and positively correlated with Q_1. The second axis Q_2 (21.2% of the total variance) reflected the flow variability. During the winter period, the first two axes explained 91.5% of the variance and similarly accounted for the flow gradient (Q_1) and the flow variability (Q_2).

Fish sampling

At the reach scale, the mean ($\pm$ SD) brown trout densities across 12 years in July ranged between 19.3 ± 11 and 78.6 ± 24.7 trout per $100\ m^2$ (Table 1), with a minimum in BO2 and a maximum in BO3. The mean ($\pm$ SD) capture probability of 0+ fish (Table 1) was significantly lower in July than in November (Wilcoxon's test; $Z = 2.86$; $P = 0.004$). For older age classes, the mean capture probability

Table 1. Mean ($\pm$ SD) brown trout densities per reach, age class and sampling month over a 12-year period (ind. 100 m^{-2}) and mean ($\pm$ SD) capture probability (p_{capt}) per age class.

Reach	0+		1+		>1+		Total	
	July	Nov	July	Nov	July	Nov	July	Nov
BO1	52.7 $\pm$ 54.6	27.0 $\pm$ 22.0	16.5 $\pm$ 14.2	8.3 $\pm$ 6.7	3.9 $\pm$ 2.4	1.5 $\pm$ 1.5	73.1 $\pm$ 52.9	36.8 $\pm$ 27.8
BO2	7.7 $\pm$ 7.3	5.4 $\pm$ 5.8	8.6 $\pm$ 7.3	6.3 $\pm$ 4.7	2.9 $\pm$ 1.6	3.2 $\pm$ 1.6	19.3 $\pm$ 11.0	14.9 $\pm$ 8.0
BO3	21.4 $\pm$ 15.5	27.3 $\pm$ 14.9	36.7 $\pm$ 15.3	30.9 $\pm$ 14.2	20.5 $\pm$ 9.1	16.4 $\pm$ 9.2	78.6 $\pm$ 24.7	74.6 $\pm$ 21.1
BO4	23.9 $\pm$ 22.8	25.1 $\pm$ 21.6	21.2 $\pm$ 13.0	15.2 $\pm$ 9.7	9.6 $\pm$ 5.2	7.5 $\pm$ 4.5	54.8 $\pm$ 31.6	47.9 $\pm$ 27.1
BO5	11.8 $\pm$ 11.8	12.0 $\pm$ 9.3	11.1 $\pm$ 9.3	8.1 $\pm$ 6.8	3.3 $\pm$ 2.6	3.0 $\pm$ 2.1	26.2 $\pm$ 18.9	23.1 $\pm$ 13.7
BO6	12.5 $\pm$ 8.8	9.4 $\pm$ 6.4	6.5 $\pm$ 4.1	5.9 $\pm$ 4.2	3.8 $\pm$ 2.3	3.9 $\pm$ 2.2	22.8 $\pm$ 9.3	19.2 $\pm$ 8.0
BO7	21.4 $\pm$ 16.2	12.0 $\pm$ 10.5	7.7 $\pm$ 5.9	5.4 $\pm$ 3.3	4.1 $\pm$ 2.6	4.4 $\pm$ 2.5	33.2 $\pm$ 21.2	21.8 $\pm$ 13.4
BO8	26.7 $\pm$ 23.7	11.0 $\pm$ 10.1	4.3 $\pm$ 2.9	3.7 $\pm$ 2.7	1.4 $\pm$ 0.8	2.2 $\pm$ 1.4	32.4 $\pm$ 24.7	16.9 $\pm$ 11.1
BO9	23.8 $\pm$ 24.8	17.5 $\pm$ 22.2	7.7 $\pm$ 6.9	5.7 $\pm$ 3.7	2.1 $\pm$ 1.0	2.2 $\pm$ 0.9	33.6 $\pm$ 25.4	25.3 $\pm$ 21.2
LE1	11.2 $\pm$ 10.7	28.2 $\pm$ 28.8	34.0 $\pm$ 16.0	25.5 $\pm$ 13.6	10.1 $\pm$ 6.6	9.0 $\pm$ 7.2	55.3 $\pm$ 17.5	62.8 $\pm$ 34.9
BT1	14.2 $\pm$ 31.1	13.9 $\pm$ 27.0	13.0 $\pm$ 18.0	7.8 $\pm$ 7.9	5.4 $\pm$ 2.4	4.3 $\pm$ 2.2	32.7 $\pm$ 33.8	26.0 $\pm$ 26.9
Mean	**20.6 $\pm$ 26.3**	**17.4 $\pm$ 19.4**	**15.2 $\pm$ 15.2**	**11.4 $\pm$ 11.6**	**6.0 $\pm$ 6.5**	**5.3 $\pm$ 5.7**	**41.9 $\pm$ 32.5**	**34.1 $\pm$ 28.2**
p_{capt}	0.77 $\pm$ 0.18	0.84 $\pm$ 0.16	0.87 $\pm$ 0.11	0.90 $\pm$ 0.11	0.91 $\pm$ 0.13	0.91 $\pm$ 0.12	0.86 $\pm$ 0.15	0.88 $\pm$ 0.14

always exceeded 0.87 for 1+ fish and 0.90 for adult fish.

Apparent survival

Several models displayed extremely similar AICc values (Table S1), especially during the first summer period. Overall, the model averaging procedure for the three studied periods mostly retained the negative (density-dependent) effect of year-class density, which displayed the highest absolute standardised estimate value among all explanatory variables (excl. interactions) together with the maximum relative importance (Table 2). Thus, apparent survival during the first summer (S_{sum0+}) was nega-

tively related to D_{0+}. Older age class ($D_{>1+}$) exerted a positive, but lower magnitude effect on S_{sum0+}. A significant interaction between Q_1 and D_{0+} was also reported. When considering sampling errors in the model selection procedure (Table 2), the results indicated that D_{0+} significantly negatively affected S_{sum0+} in 65.9% of the implemented simulations (Z tests, $P < 0.05$), which questioned the robustness of the density-dependent survival relationship. Conversely, the interaction between Q_1 and D_{0+} was significant in 97.5% of the simulations. This interaction indicated that for low-flow values, S_{sum0+} and D_{0+} exhibited a negative relationship, whereas no relationship appeared at a higher mean flow (Fig. 2).

Table 2. Model averaging for log-transformed apparent survival during each studied period (first summer, first winter and second summer). Estimates (standardised averaged coefficients) were provided within a 95% confidence interval (CI) and with significant P-values (*** $P < 0.001$, ** $P < 0.01$ and * $P < 0.05$). The relative importance (Imp) of each parameter is indicated. The effect of simulated sampling error (10,000 iterations) on the significance of the parameters in the linear model (LM) or linear mixed model (LMM) is reported.

Period	N	Model	Fixed factor	Without sampling error			Simulated sampling error	
				Estimate	CI	Imp	Mean estimate	% Significant estimates
1st summer	71	LM	(intercept)	0.589***	[0.554, 0.624]			
			D_{0+}	−0.141***	[−0.215, −0.068]	1.00	−0.125	65.9
			D_{1+}	0.045	[−0.047, 0.137]	0.25	0.045	2.9
			$D_{>1+}$	0.120**	[0.040, 0.200]	1.00	0.110	50.1
			Q_1	0.067	[−0.008, 0.141]	1.00	0.103	47.5
			Q_2	−0.059*	[−0.147, −0.001]	1.00	−0.090	11.2
			T_1	−0.040	[−0.123, 0.043]	0.57	−0.028	0.8
			D_{0+} :Q_1	0.245**	[0.088, 0.402]	1.00	0.334	97.5
1st winter	73	LMM	(Random intercept)	0.571***	[0.492, 0.649]			
			D_{0+}	−0.158***	[−0.224, −0.092]	1.00	−0.192	100.0
			$D_{>1+}$	0.044	[−0.028, 0.116]	0.37	0.045	2.1
2nd summer	93	LM	(Intercept)	0.560***	[0.529, 0.590]			
			D_{0+}	−0.068	[−0.136, 0.001]	0.63	−0.065	35.6
			D_{1+}	−0.125**	[−0.201, −0.050]	1.00	−0.132	100.0
			$D_{>1+}$	0.094*	[0.020, 0.168]	1.00	0.097	99.4
			Q_1	0.074*	[0.007, 0.140]	1.00	0.077	82.4
			Q_2	−0.025	[−0.093, 0.043]	0.18	−0.023	0.0
			T_2	−0.068	[−0.139, 0.004]	0.82	−0.069	33.3
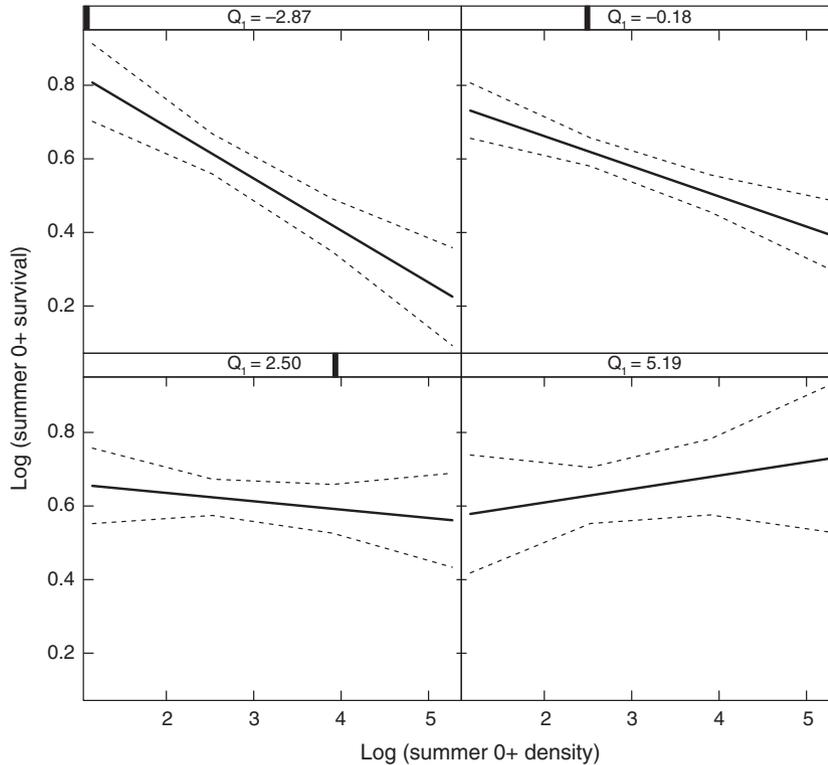
Fig. 2. Interactive effects of the 0+ density and mean flow (accounted for by Q_1) on 0+ summer survival. Dashed lines represent the confidence bands at 95%.

Apparent winter survival (S_{win0+}) was negatively related to D_{0+} in autumn (Fig. 3). This negative density-dependent relationship remained significant in 100% of the trials when simulating density estimate uncertainties (Table 2). Both the year and reach random effects were significant (likelihood-ratio tests on random intercepts; *LR Chisq* = 3.49, *P* = 0.031 and *LR Chisq* = 6.45, *P* = 0.006 for year and reach effect, respectively).

After the second summer, the apparent survival of the 1+ age class (S_{sum1+}) was negatively related to

Fig. 3. Relationship between winter apparent survival of 0+ individuals and 0+ density in autumn ($N = 73$; $y = 1.178\,x^{-0.178}$; $R^2 = 0.124$).

the 1+ initial density D_{1+} and positively related to $D_{>1+}$ and Q_1. Because Q_1 primarily accounted for the mean and maximum daily flows, a low summer flow resulted in lower S_{sum1+}. Considering sampling error, parameter estimates remained fairly constant across simulations, most likely due to the good capture efficiency for fish of this age class in all censuses (Table 1). Juvenile and adult densities were significant in 100 and 99.4% of the simulations, respectively, and Q_1 was significant in 82.4% of the simulations.

Total length

The initial age class density negatively affected the mean total length for the three studied periods (Table 3). The 0+ mean length at the end of the first summer (L_{nov0+}) was negatively related to both D_{0+} and D_{1+}. Q_1 and T_1 positively affected the L_{nov0+}, where higher mean flows and temperatures yielded larger fish at the end of the first summer. A random 'reach' effect was also significant (Likelihood-ratio test; *LR Chisq* = 23.69, *P* < 0.001).

At the end of the first winter period, the mean total length of the 1+ age class (L_{juil1+}) was negatively related to D_{0+} and to a lesser extent positively related to T_1. Random reach and year effects were significant (LR tests on random intercept; *LR Chisq* = 30.74, *P* < 0.001 and *LR Chisq* = 14.52,

7

Table 3. Model averaging of the log-transformed mean total length (L) and coefficient of variation for length (CV) after each of the three studied period: first summer (0+), first winter (0+ to 1+) and second summer (1+). Estimates (standardised averaged coefficients) are provided within a 95% confidence interval (CI) and with significant P-values (*** $P < 0.001$, ** $P < 0.01$ and * $P < 0.05$). The relative importance (Imp) of each parameter is also indicated.

Dependent variable	Parameter	First summer			First winter			Second summer		
		Estimate	CI	Imp	Estimate	CI	Imp	Estimate	CI	Imp
L	Intercept	4.455***	[4.420, 4.491]		4.907***	[4.853, 4.960]		4.994***	[4.951, 5.037]	
	D_{0+}	−0.108***	[−0.141, −0.075]	1.00	−0.105***	[−0.130, −0.080]	1.00	−0.012	[−0.046, 0.023]	0.16
	D_{1+}	−0.049*	[−0.087, −0.010]	1.00	−0.024	[−0.056, 0.008]	0.38	−0.081***	[−0.123, −0.039]	1.00
	$D_{>1+}$	−0.019	[−0.063, 0.024]	0.19	−0.019	[−0.049, 0.011]	0.32			
	Q_1	0.104***	[0.071, 0.138]	1.00	0.031	[−0.014, 0.076]	0.35	0.075**	[0.024, 0.126]	1.00
	Q_2	−0.015	[−0.044, 0.015]	0.21						
	T_1	0.119***	[0.054, 0.184]	1.00	0.086*	[0.008, 0.163]	0.52	0.082*	[0.006, 0.158]	0.80
	T_2	−0.013	[−0.046, 0.020]	0.17	0.028	[−0.023, 0.079]	0.18	0.021	[−0.025, 0.068]	0.19
CV	Intercept	0.126***	[0.120, 0.132]		0.117***	[0.112, 0.121]		0.102***	[0.092, 0.112]	
	D_{0+}	0.019**	[0.006, 0.031]	1.00	0.019***	[0.009, 0.030]	1.00	0.005	[−0.007, 0.017]	0.15
	D_{1+}	0.013	[−0.000, 0.026]	0.72	0.006	[−0.005, 0.017]	0.38	0.007	[−0.007, 0.021]	0.18
	$D_{>1+}$							0.017*	[0.003, 0.030]	1.00
	T_1	−0.007	[−0.021, 0.006]	0.30	−0.014**	[−0.025, −0.004]	1.00	0.010	[−0.008, 0.028]	0.19
	T_2							−0.012*	[−0.023, −0.001]	1.00
	Q_1	0.006	[−0.007, 0.020]	0.19	−0.008	[−0.018, 0.002]	0.55			
	Q_2	0.014*	[0.001, 0.027]	1.00				0.004	[−0.008, 0.015]	0.14

$P < 0.001$, respectively). The relationship between L_{juil1+} and D_{0+} was negative for 10 of 11 reaches (Fig. 4) and for all 11 years.

At the end of the second summer (1+ age class), the juvenile initial density (D_{1+}), Q_1 and T_1 were strongly selected in the averaged model of mean length (L_{nov1+}). The main effect was due to the negative density-dependent relationship between D_{1+} and L_{nov1+}. The mean summer flow Q_1 and mean temperature T_1 both positively influenced L_{nov1+}. Random reach and year effects were significant (*LR Chisq* = 14.68, $P < 0.001$; *LR Chisq* = 4.55, $P = 0.016$).

Coefficient of variation for 0+ length

The coefficient of variation for the 0+ length at the end of the first summer (CV_{nov0+}) increased with increasing initial 0+ density (Table 3). The initial density of 1+ (D_{1+}) was also positively related to CV_{nov0+} (Imp = 0.72). The flow variability (Q_2) also positively affected the 0+ size variation at the end of the summer.

At the end of the winter period, the coefficient of variation for 1+ length (CV_{juil1+}) was positively related to the D_{0+} from the previous autumn and negatively related to the T_1. Per reach analysis (Fig. 5) exhibited a similar pattern of positive relationships between the D_{0+} and CV_{juil1+} in all 11 reaches.

At the end of the second summer, the CV_{nov1+} did not correlate with the initial density of 1+ individuals but was positively related to the adult (>1+) density (Table 3). The temperature variable T_2 negatively influenced the size variation of 1+ fish during the summer. A random reach effect was significant for this second summer (LR test, *LR Chisq* = 7.17, $P = 0.004$).

Discussion

Analysis of the low-density brown trout population of the Boiron River revealed that both density-dependent and density-independent regulations were operating on the apparent survival, mean size and size variability of 0+ and 1+ fish (i.e., from the first summer to the end of the second summer).

Density-dependent mortality has been described as a major mechanism of salmonid population regulation that occurs shortly after emergence (Elliott 1994; Milner et al. 2003), when fish compete for food and space. Thereafter, density-independent survival was reported (Elliott 1985), at least until the second summer (Lobón-Cerviá 2012). In our study, apparent survival of the 0+ and 1+ fish was predominantly affected by the initial density of the respective age class, suggesting a density-dependent regulation through intracohort competition. This result agrees with Newman (1993), who observed that the loss rate (mortality and/or emigration) of 0+ brown trout from their first summer to the following spring was density-dependent. A bottleneck during winter occurs in some salmonid populations due to limited resources (Cunjak & Power 1987) or low shelter availability (Armstrong & Griffiths 2001) that increases vulnerability to predators. However, this phenomenon does not seem to be a rule, as Carlson et al. (2008) did not observe additional over-winter mortality in brown trout populations. Density-dependent mortality was
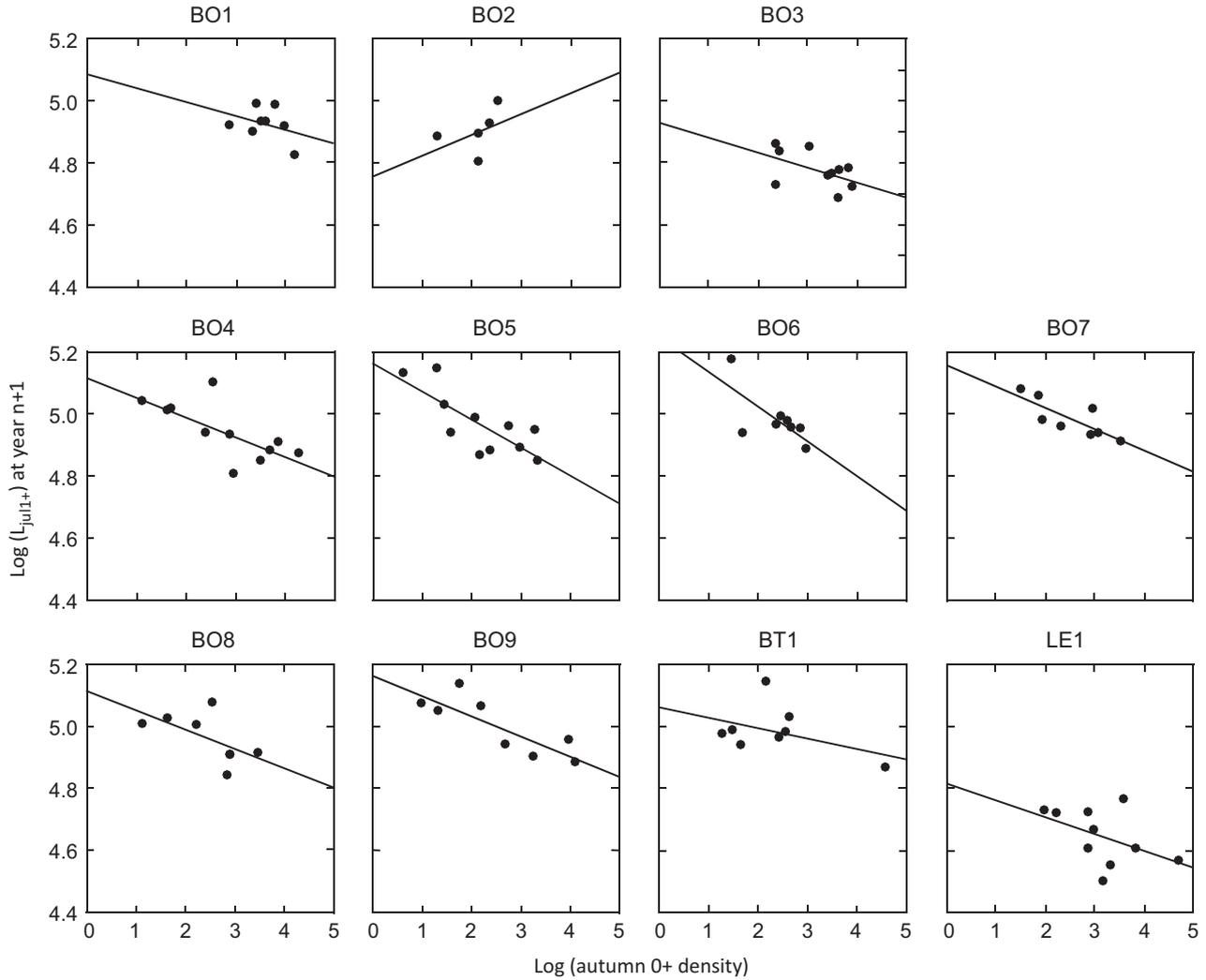
Fig. 4. Relationships per reach between 1+ mean length in the summer (L_{jul1+}) and 0+ densities of the previous autumn.

also observed later in life at the yearling (1+) or adult (>1+) stages (Carline 2006; Vøllestad & Olsen 2008; Lobón-Cerviá 2012).

The models on apparent survival were tested by simulating density estimate uncertainties. In our sampling, most uncertainties arose from the size-bias of electrofishing (i.e., lower capture efficiency of small fish) but also from the relatively short length (in a population dynamics context; 12 years) of our time-series data (Lebreton & Gimenez 2013). Simulations clearly demonstrated that density estimate uncertainties could question the strength of the relationship between survival and age class densities, especially during the first summer of the 0+ stage. However, the interaction between 0+ density and the flow variable Q_1 (accounting for mean flow over each period) remained highly significant in almost all simulations. Density affected apparent survival during low-flow years, whereas low or no density dependence was detected under high mean flow. Conversely, Vøllestad & Olsen (2008) reported a lower apparent

survival of 1+ brown trout at low flow, which was independent from the initial density; under intermediate to higher flow, the apparent survival was density-dependent. The authors hypothesised that drought stress was the major process regulating populations, and under normal flow conditions, density dependence occurred. Over the 12 years of the present study, no exceptional drought conditions occurred; however, low flow, especially during the first summer, enhanced the strength of density-dependent regulation on apparent survival. During the second summer, a negative effect of low flow on the apparent survival of 1+ fish was also detected, as previously observed by Elliott et al. (1997) for age 0+ and 1+ sea trout *S. trutta* after summer droughts. Low flow reduced habitat quality and quantity, which potentially lead to a higher mortality, especially in reaches with low pool areas (Hakala & Hartman 2004).

The underlying processes explaining the density-dependent apparent survival of 0+ and 1+ fish in the
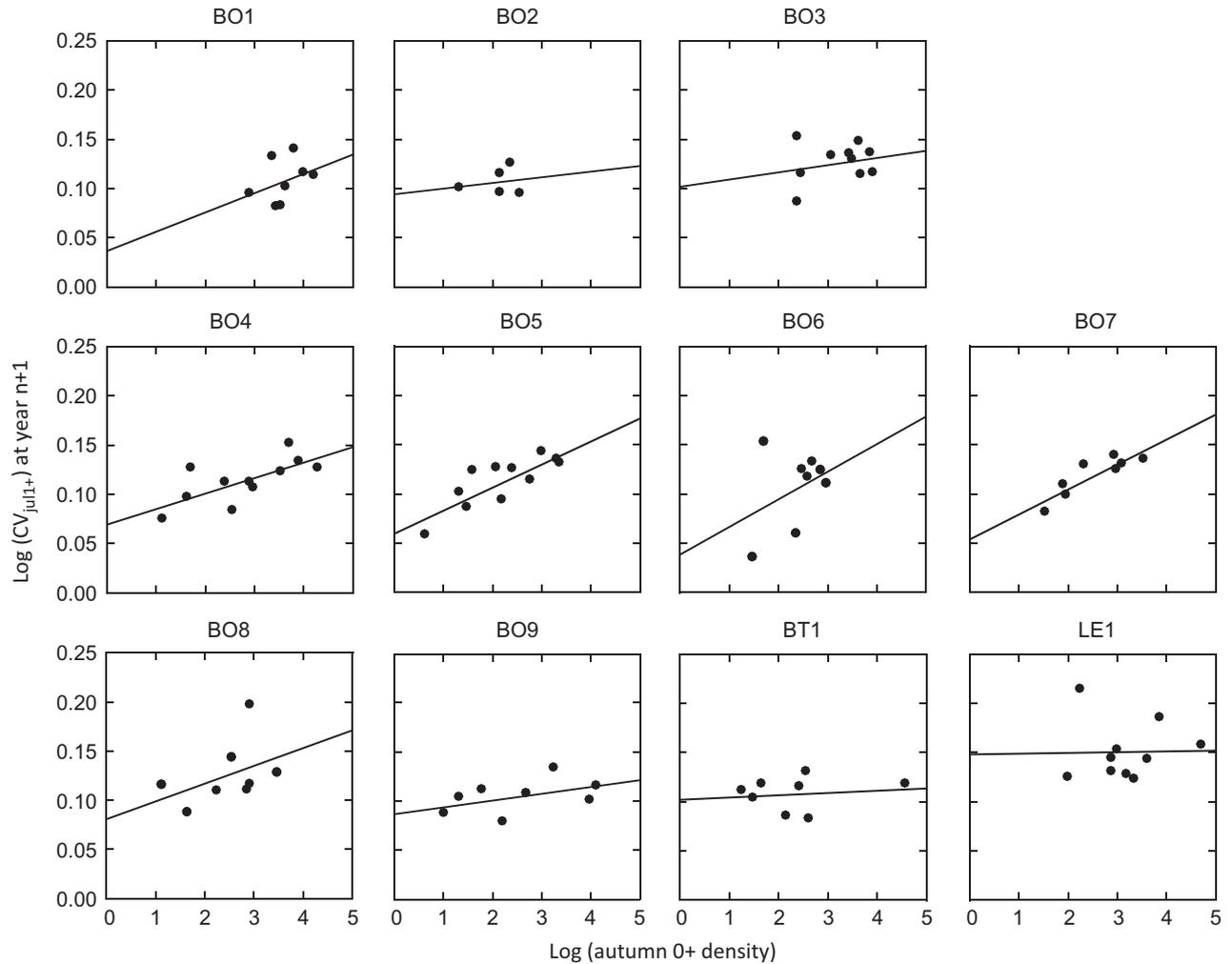
Fig. 5. Relationships per reach between the coefficient of variation for length of 1+ fish in the summer (CV_{jul1+}) and 0+ densities of the previous autumn.

Boiron River are unknown. The absence of significant intercohort effect suggests more spatial habitat segregation than diet partitioning between cohorts, because 0+ and 1+ fish feeding niches generally overlap (Kaspersson & Höjesjö 2009). Stream-dwelling salmonids generally compete *via* interference, while defending the most valuable feeding territories (Grant 1997). In the Boiron, summers are often characterised by long periods of low flow, therefore gathering fish in restricted microhabitats. This probably increased aggression and competition for food and shelters. Also, the predation by avian predators, such as herons *Ardea cinerea* and kingfisher *Alcedo atthis* (which have both been observed along the river), may be increased during low-flow periods. Finally, migration could also be responsible for the lower apparent survival observed. Einum et al. (2006) demonstrated that the 0+ density did not affect summer survival but strongly affected dispersal. Although our data did not allow disentangling the respective parts of real mortality and migration, we cannot exclude

that the lower apparent survival could result from a general pattern of downstream migration, even though stream-dwelling YOY brown trout generally display restricted movement (Kaspersson & Höjesjö 2009).

Density-dependent growth was reported for the three studied periods. This is consistent with other studies that revealed a negative power relationship between body size or weight and 0+ fish density in low-density brown trout (Lobon-Cervia 2007a) and salmon populations (Imre et al. 2005). Therefore, an increase of density would yield greater effects on mean length under low densities. In our study, mean fish growth was regulated both by intra- and intercohort competitions, especially during the first summer, and the relationships were consistent between years and reaches. Yearling (1+) densities affected YOY growth, as observed in other brown trout populations (Nordwall et al. 2001; Lobón-Cerviá 2005; Kaspersson & Höjesjö 2009). Intercohort densities (≥1+) during the first year of marble trout life determined the

mean length and weight of the year-class throughout their lifetime (Vincenzi et al. 2008b, 2010a), suggesting that growth trajectories are determined early in life. However, Vincenzi et al. (2008b) did not assess 0+ densities, which were reported as the major effectors of the growth of 0+ individuals in the present study, as well as in Atlantic salmon populations (Imre et al. 2005). Conversely, we did not detect any effect of the 0+ density on the growth of age 1+ as reported by Kvingedal & Einum (2011). During the first summer, 0+ and 1+ individuals presumably compete for the same feeding territories at the expense of the growth of 0+ fish. The exclusion of 0+ fish from the preferred habitats and shelters by older cohorts was usually reported during the first summer (Kaspersson et al. 2012) and the first winter (Vehanen et al. 1999). In our study, the mean length after the first winter and second summer were mostly related to intracohort density.

Size variation around the mean (CV of body length) was also positively related to 0+ fish density after the first summer and the first winter period, which was consistent in almost all reaches. Increasing size variation with density has already been reported in low-density salmonid populations (Jenkins et al. 1999; Einum et al. 2006; Lobón-Cerviá 2010), although the shape of the relationship (i.e., linear or power function) is uncertain (Lobón-Cerviá 2010). Following Newman's (1993) site-quality model, higher within-cohort densities would lead to an increase of slow-growing fish (relegated to less valuable places), thus resulting in a greater variation in fish size. In our study, the CV was no more related to the age class density after the second summer (1+ fish). Nordwall et al. (2001) demonstrated an inverse (negative) relationship between the CV and 1+ fish density in resident brown trout populations, which was explained by an increased mortality of slow-growing fish during the first year of life. Although the underlying mechanisms cannot be elucidated from the observed data, we hypothesise that a size-dependent mortality (i.e., impacting slow-growing fish) occurred after the first winter, which mitigated the positive relationship between CV and density. This would be in accordance with Lobón-Cerviá (2012), who demonstrated an increased mortality after the first year.

In addition to the biotic regulation, the mean temperature and flow were positively related to the mean fish size during the summer season. The relationship between brown trout growth and water temperature has been widely reported and modelled (e.g., Elliott & Elliott 1995; Nicola & Almodóvar 2004). Parra et al. (2012) demonstrated a positive effect of water temperature on growth, even though high-temperature values provoked deleterious effects, especially during the first year of life. In the Boiron River, mean daily temperatures remained in a range suitable for brown trout growth (Elliott & Elliott 2010), although maximum temperatures sometimes exceeded 20 °C in the downstream reaches during the summer. The positive effect of temperature was stronger during the first summer than in the two following periods. This is consistent with Parra et al. (2012), who showed that temperature was a strong determinant for 0+ growth, whereas for older age classes, density-dependent regulation was the primary process acting on growth.

The flow level during summer was positively related to 0+ and 1+ fish length. A reduced summer flow constrains fish in a restricted habitat, where fish compete for the most profitable position. Vøllestad & Olsen (2008) showed that summer droughts negatively affected brown trout individual growth in a Norwegian stream. Juvenile brown trout generally display a drift-feeding behaviour (Glova & Field-Dodgson 1995). With higher flows, the number of drifting preys becoming available to fish increases together with the number of favourable foraging locations, thus presumably increasing mean fish growth (Nislow et al. 2004; Vøllestad & Olsen 2008). Teichert et al. (2010) manipulated flow and juvenile Atlantic salmon in artificial streams and demonstrated a similar positive relationship between growth and discharge (or mean velocity) during the summer. Conversely, during the winter, they reported negative fish growth rates, which were neither related to flow variations nor density. In the present study, flow parameters were not retained by the model during the winter season. Low-flow periods during summer reduce the availability of feeding territories for juvenile brown trout that in turn could increase the competition for resources.

The biotic and abiotic regulation of body size experienced at the juvenile stage (first two years of life) may have subsequent effects on population dynamics. Early conditions could determine later growth trajectories (e.g., Vincenzi et al. 2010a), which could influence individual fitness. Body size is related to different life history traits, such as age at maturity, fecundity, egg size and survival (Vincenzi et al. 2012). For example, the number of eggs produced by 1+ females correlated with fish size and was determined during the first year in brown trout populations from the Esva River basin, Spain (Lobon-Cervia et al. 1997). At a lower density, compensatory increases in body growth induced a faster sexual maturation and a higher *per capita* egg production (Vincenzi et al. 2010b). Jenkins et al. (1999) hypothesised that density-dependent growth could allow brown trout populations to recover quickly after major catastrophic events leading to high mortality rates. Vincenzi et al. (2008a) demonstrated that

because density-dependent growth occurred, the resilience of marble trout populations increased after severe floods. We also revealed that the apparent survival at the juvenile stage (0+ and 1+ fish) increased when the density was lower, which could be a powerful mechanism to quickly restore a higher population size after a major disturbance. Density-dependent mechanisms acting on both apparent survival and growth can presumably foster population recovery in harsh or occasionally disturbed environments (i.e., after floods, rain-on-snow events, droughts or point pollutions) and increase population resilience.

The originality of this study relies on coupling population data collected at multiple sites over 12 years with environmental features to investigate the factors driving population dynamics. This approach did not address the causes of the observed density-dependent processes. Inferring the nature of the mechanism involved (either limitation by food or space, or both) from empirical studies may be misleading and requires well-designed experimental studies (Ward et al. 2007). However, we clearly demonstrated the major role of biotic processes in the regulation of apparent survival, mean length and CV, for three juvenile stages (first summer, first winter and second summer). The strong interacting effect of flow and trout density on apparent survival highlighted the need for jointly analysing the roles of biotic and abiotic factors. Although density-dependent and density-independent processes act simultaneously on brown trout populations, biotic processes (both intra- and intercohort) are the prevailing effects in the Boiron River, presumably in the absence of major climatic events (extreme droughts, spates).

Acknowledgements

References

Armstrong, J.D. & Griffiths, S.W. 2001. Density-dependent refuge use among over-wintering wild Atlantic salmon juveniles. Journal of Fish Biology 58: 1524–1530.

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M. & Milner, N.J. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fisheries Research 62: 143–170.

Bærum, K.M., Haugen, T.O., Kiffney, P., Moland Olsen, E. & Vøllestad, L.A. 2013. Interacting effects of temperature and density on individual growth performance in a wild population of brown trout. Freshwater Biology 58: 1329–1339.

Bal, G., Rivot, E., Prévost, E., Piou, C. & Baglinière, J.L. 2011. Effect of water temperature and density of juvenile salmonids on growth of young-of-the-year Atlantic salmon Salmo salar. Journal of Fish Biology 78: 1002–1022.

Barton, K. 2013. MuMIn: Multi-model inference. R package version 1.9.5. URL http://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf.

Brook, B.W. & Bradshaw, C.J.A. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. Ecology 87: 1445–1451.

Burnham, K.P. & Anderson, D.R. 2002. Model selection and multi-model inference. New York: Springer-Verlag.

Carle, F.L. & Strub, M.R. 1978. A new method for estimating population size from removal data. Biometrics 34: 621–630.

Carline, R.F. 2006. Regulation of an unexploited brown trout population in Spruce Creek, Pennsylvania. Transactions of the American Fisheries Society 135: 943–954.

Carlson, S.M., Olsen, E. M. & Vøllestad, L.A. 2008. Seasonal mortality and the effect of body size: a review and an empirical test using individual data on brown trout. Functional Ecology 22: 663–673.

Cattanéo, F., Lamouroux, N., Breil, P. & Capra, H. 2002. The influence of hydrological and biotic processes on brown trout (Salmo trutta) population dynamics. Canadian Journal of Fisheries and Aquatic Sciences 59: 12–22.

Clews, E., Durance, I., Vaughan, I.P. & Ormerod, S.J. 2010. Juvenile salmonid populations in a temperate river system track synoptic trends in climate. Global Change Biology 16: 3271–3283.

Crisp, D.T. 1993. Population densities of juvenile trout (Salmo trutta) in five upland streams and their effects upon growth, survival and dispersal. Journal of Applied Ecology 30: 759–771.

Crozier, L.G., Zabel, R.W., Hockersmith, E.E. & Achord, S. 2010. Interacting effects of density and temperature on body size in multiple populations of Chinook salmon. Journal of Animal Ecology 79: 342–349.

Cunjak, R.A. & Power, G. 1987. The feeding and energetics of stream-resident trout in winter. Journal of Fish Biology 31: 493–511.

Cunjak, R.A., Linnansaari, T. & Caissie, D. 2013. The complex interaction of ecology and hydrology in a small catchment: a salmon's perspective. Hydrological Processes 27: 741–749.

Einum, S. & Nislow, K.H. 2005. Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. Oecologia 143: 203–210.

Einum, S., Sundt-Hansen, L. & Nislow, K.H. 2006. The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. Oikos 113: 489–496.

Elliott, J.M. 1985. Population regulation for different life-stages of migratory trout Salmo trutta in a lake district stream, 1966–83. Journal of Animal Ecology 54: 617–638.

Elliott, J.M. 1994. Quantitative ecology and the brown trout. Oxford: Oxford University Press. 286 pp.

Elliott, J.M. & Elliott, J.A. 1995. The effect of the rate of temperature increase on the critical thermal maximum for parr of Atlantic salmon and brown trout. Journal of Fish Biology 47: 917–919.

Elliott, J.M. & Elliott, J.A. 2010. Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. Journal of Fish Biology 77: 1793–1817.

Elliott, J.M., Hurley, M.A. & Elliott, J.A. 1997. Variable effects of droughts on the density of a sea-trout *Salmo trutta* population over 30 years. Journal of Applied Ecology 34: 1229–1238.

Fox, J. 2003. Effect displays in R for generalised linear models. Journal of Statistical Software 8: 1–27.

Gelman, A. & Su, Y.-S., 2013. arm: data analysis using regression and multilevel/hierarchical models. R package version 1.6-09. http://CRAN.R-project.org/package=arm.

Glova, G.J. & Field-Dodgson, M.S. 1995. Behavioral interaction between Chinook salmon and brown trout juveniles in a simulated stream. Transactions of the American Fisheries Society 124: 194–206.

Grant, J.W.A. 1997. Territoriality. In: Behavioral ecology of teleost fishes (Godin, J.-G.J., ed.). Oxford: Oxford University Press, pp. 81–103.

Grant, J.W.A. & Imre, I. 2005. Patterns of density-dependent growth in juvenile stream-dwelling salmonids. Journal of Fish Biology 67: 100–110.

Grant, J.W.A. & Kramer, D.L. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Canadian Journal of Fisheries and Aquatic Sciences 47: 1724–1737.

Grossman, G.D., Ratajczak, R.E., Wagner, C.M. & Petty, J.T. 2010. Dynamics and regulation of the southern brook trout (*Salvelinus fontinalis*) population in an Appalachian stream. Freshwater Biology 55: 1494–1508.

Grossman, G.D., Nuhfer, A., Zorn, T., Sundin, G. & Alexander, G. 2012. Population regulation of brook trout (*Salvelinus fontinalis*) in Hunt Creek, Michigan: a 50-year study. Freshwater Biology 57: 1434–1448.

Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24: 699–711.

Hakala, J.P. & Hartman, K.J. 2004. Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. Hydrobiologia 515: 203–213.

Imre, I., Grant, J.W.A. & Cunjak, R.A. 2005. Density-dependent growth of young-of-the-year Atlantic salmon *Salmo salar* in Catamaran Brook, New Brunswick. Journal of Animal Ecology 74: 508–516.

Imre, I., Grant, J.W.A. & Cunjak, R.A. 2010. Density-dependent growth of young-of-the-year Atlantic salmon (*Salmo salar*) revisited. Ecology of Freshwater Fish 19: 1–6.

Jenkins, T.M., Diehl, S., Kratz, K.W. & Cooper, S.D. 1999. Effects of population density on individual growth of brown trout in streams. Ecology 80: 941–956.

Jensen, A.J., Forseth, T. & Johnsen, B.O. 2000. Latitudinal variation in growth of young brown trout *Salmo trutta*. Journal of Animal Ecology 69: 1010–1020.

Jonsson, N., Jonsson, B. & Hansen, L.P. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. Journal of Animal Ecology 67: 751–762.

Kaspersson, R. & Höjesjö, J. 2009. Density-dependent growth rate in an age-structured population: a field study on stream-dwelling brown trout *Salmo trutta*. Journal of Fish Biology 74: 2196–2215.

Kaspersson, R., Höjesjö, J. & Bohlin, T. 2012. Habitat exclusion and reduced growth: a field experiment on the effects of inter-cohort competition in young-of-the-year brown trout. Oecologia 169: 733–742.

Keeley, E.R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. Ecology 82: 1247–1259.

Keller, E.A. & Melhorn, W.N. 1978. Rhythmic spacing and origin of pools and riffles. Geological Society of America Bulletin 89: 723–730.

Kvingedal, E. & Einum, S. 2011. Intracohort and intercohort spatial density dependence in juvenile brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 68: 115–121.

Lamouroux, N. & Capra, H. 2002. Simple predictions of instream habitat model outputs for target fish populations. Freshwater Biology 47: 1543–1556.

Lebreton, J.-D. & Gimenez, O. 2013. Detecting and estimating density dependence in wildlife populations. The Journal of Wildlife Management 77: 12–23.

Lobon-Cervia, J. 2007a. Density-dependent growth in stream-living Brown Trout *Salmo trutta* L. Functional Ecology 21: 117–124.

Lobon-Cervia, J. 2007b. Numerical changes in stream-resident brown trout (*Salmo trutta*): uncovering the roles of density-dependent and density-independent factors across space and time. Canadian Journal of Fisheries and Aquatic Sciences 64: 1429–1447.

Lobón-Cerviá, J. 2004. Discharge-dependent covariation patterns in the population dynamics of brown trout (*Salmo trutta*) within a Cantabrian river drainage. Canadian Journal of Fisheries and Aquatic Sciences 61: 1929–1939.

Lobón-Cerviá, J. 2005. Spatial and temporal variation in the influence of density dependence on growth of stream-living brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 62: 1231–1242.

Lobón-Cerviá, J. 2010. Density dependence constrains mean growth rate while enhancing individual size variation in stream salmonids. Oecologia 164: 109–115.

Lobón-Cerviá, J. 2012. Density-dependent mortality in adults, but not juveniles, of stream-resident brown trout (*Salmo trutta*). Freshwater Biology 57: 2181–2189.

Lobon-Cervia, J., Utrilla, C., Rincón, P. & Amezcua, F. 1997. Environmentally induced spatio-temporal variations in the fecundity of brown trout *Salmo trutta* L.: trade-offs between egg size and number. Freshwater Biology 38: 277–288.

Logez, M. & Pont, D. 2011. Variation of brown trout *Salmo trutta* young-of-the-year growth along environmental gradients in Europe. Journal of Fish Biology 78: 1269–1276.

Malavoi, J.R. & Souchon, Y. 2002. Standardized description of streams and rivers channel geomorphic units: qualitative description key and physical measurements (French). Bulletin Français de la Pêche et de la Pisciculture 365/366: 357–372.

Milner, N.J., Elliott, J.M., Armstrong, J.D., Gardiner, R., Welton, J.S. & Ladle, M. 2003. The natural control of salmon and trout populations in streams. Fisheries Research 62: 111–125.

Newman, R.M. 1993. A conceptual model for examining density dependence in the growth of stream trout. Ecology of Freshwater Fish 2: 121–131.

Nicola, G.G. & Almodóvar, A. 2004. Growth pattern of stream-dwelling brown trout under contrasting thermal conditions. Transactions of the American Fisheries Society 133: 66–78.

Nislow, K.H. & Armstrong, J.D. 2012. Towards a life-history-based management framework for the effects of flow on juvenile salmonids in streams and rivers. Fisheries Management and Ecology 19: 451–463.

Nislow, K.H., Sepulveda, A.J. & Folt, C.L. 2004. Mechanistic linkage of hydrologic regime to summer growth of age-0 Atlantic salmon. Transactions of the American Fisheries Society 133: 79–88.

Nordwall, F., Näslund, I. & Degerman, E. 2001. Intercohort competition effects on survival, movement, and growth of brown trout (Salmo trutta) in Swedish streams. Canadian Journal of Fisheries and Aquatic Sciences 58: 2298–2308.

Parra, I., Almodóvar, A., Ayllón, D., Nicola, G. & Elvira, B. 2012. Unravelling the effects of water temperature and density dependence on the spatial variation of brown trout (Salmo trutta) body size. Canadian Journal of Fisheries and Aquatic Sciences 69: 821–832.

R Development Core Team.2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Teichert, M.A.K., Kvingedal, E., Forseth, T., Ugedal, O. & Finstad, A.G. 2010. Effects of discharge and local density on the growth of juvenile Atlantic salmon Salmo salar. Journal of Fish Biology 76: 1751–1769.

Unfer, G., Hauer, C. & Lautsch, E. 2011. The influence of hydrology on the recruitment of brown trout in an Alpine river, the Ybbs river, Austria. Ecology of Freshwater Fish 20: 438–448.

Vehanen, T., Mäki-Petäys, A., Aspi, J. & Muotka, T. 1999. Intercohort competition causes spatial segregation in brown trout in artificial streams. Journal of Fish Biology 55: 35–46.

Vincenzi, S., Crivellò, A., Jesensek, D., Rubin, J.-F. & De Leo, G. 2007. Density-dependent individual growth of marble trout (Salmo marmoratus) in the Soca and Idrijca river basins, Slovenia. Hydrobiologia 583: 57–68.

Vincenzi, S., Crivelli, A., Jesensek, D. & De Leo, G. 2008a. The role of density-dependent individual growth in the persistence of freshwater salmonid populations. Oecologia 156: 523–534.

Vincenzi, S., Crivelli, A.J., Jesensek, D. & De Leo, G.A. 2008b. Total population density during the first year of life as a major determinant of lifetime body-length trajectory in marble trout. Ecology of Freshwater Fish 17: 515–519.

Vincenzi, S., Crivelli, A.J., Jesensek, D. & De Leo, G.A. 2010a. Detection of density-dependent growth at two spatial scales in marble trout (Salmo marmoratus) populations. Ecology of Freshwater Fish 19: 338–347.

Vincenzi, S., Crivelli, A.J., Jesensek, D. & De Leo, G.A. 2010b. Individual growth and its implications for the recruitment dynamics of stream-dwelling marble trout (Salmo marmoratus). Ecology of Freshwater Fish 19: 477–486.

Vincenzi, S., Satterthwaite, W. & Mangel, M. 2012. Spatial and temporal scale of density-dependent body growth and its implications for recruitment, population dynamics and management of stream-dwelling salmonid populations. Reviews in Fish Biology and Fisheries 22: 813–825.

Vøllestad, L.A. & Olsen, E.M. 2008. Non-additive effects of density-dependent and density-independent factors on brown trout vital rates. Oikos 117: 1752–1760.

Ward, D.M., Nislow, K.H., Armstrong, J.D., Einum, S. & Folt, C.L. 2007. Is the shape of the density–growth relationship for stream salmonids evidence for exploitative rather than interference competition? Journal of Animal Ecology 76: 135–138.

Zorn, T.G. & Nuhfer, A.J. 2007. Influences on brown trout and brook trout population dynamics in a Michigan river. Transactions of the American Fisheries Society 136: 691–705.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. New York: Springer.

Supporting Information

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

Figure S1. Projections of river temperature during the (a) summer and (b) winter for the first and second PCA components.

Figure S2. Projections of river flow measured at the outlet of the Boiron River during the (a) summer and (b) winter for the first and second PCA components.

Table S1. Model selection based on the AICc for survival (S), mean length (L) and coefficient of variation for length (CV) during the three juvenile periods (first summer, first winter and second summer).