

# Detection of density-dependent growth at two spatial scales in marble trout (*Salmo marmoratus*) populations

Vincenzi S, Crivelli AJ, Jesensek D, De Leo GA. Detection of density-dependent growth at two spatial scales in marble trout (*Salmo marmoratus*) populations.

Ecology of Freshwater Fish 2010: 19: 338–347. © 2010 John Wiley & Sons A/S

**Abstract** – Density-dependent body growth has often been observed in freshwater salmonid populations. Several studies suggest this compensatory pattern as a potential mechanism of population regulation. The choice of the spatial scale is important for the detection of density-dependent growth, as study areas need to be of the appropriate size to capture the density of conspecifics actually experienced by individuals over the preceding growth period. Here, we used four marble trout (*Salmo marmoratus*) populations (Gatsnik, Gorska, Huda and Zakojska) living in Slovenian stream to study the relationships between early density of marble trout and subsequent body growth. As streams are divided in sectors delimited by natural barriers that prevent or strongly limit movement of individuals, we tested the relationship between early density and body size through the lifetime at two spatial scales, that is, *sector* level (for Gatsnik and Zakojska) and *whole stream* level (the four populations were pooled). Sector length in Gatsnik and Zakojska ranged from 113 to 516 m. At both *sector* and *whole stream* level, temporal data were pooled. Growth declined significantly with increasing density both at the *sector* and *whole stream* levels, and the density-dependent relationship was described by negative power curves. However, at the *sector* level the density-dependent pattern was stronger in Gatsnik, a stream in which fish could move across sectors, than in Zakojska, where upstream movement across sectors is prevented by waterfalls.

**S. Vincenzi<sup>1</sup>, A. J. Crivelli<sup>2</sup>,  
D. Jesensek<sup>3</sup>, G. A. De Leo<sup>1</sup>**

<sup>1</sup>Dipartimento di Scienze Ambientali, Università degli Studi di Parma, Viale G.P. Usberti 33/A, I-43100 Parma, Italy, <sup>2</sup>Station Biologique de la Tour du Valat, Le Sambuc, F-13200, Arles, France, <sup>3</sup>Tolmin Angling Association, Modrej 26a, 65216 Most na Soci, Slovenia

**Key words:** marble trout; body growth; early density; spatial scale; negative relationship

Simone Vincenzi, Dipartimento di Scienze Ambientali, Università degli Studi di Parma, Viale G.P. Usberti 33/A I-43100 Parma, Italy; e-mail: svincenz@nemo.unipr.it

Accepted for publication March 4, 2010

## Introduction

Density-dependent growth has been reported for several species of salmonids, both anadromous (e.g., Imre et al. 2005) and freshwater resident (e.g., Jenkins et al. 1999; Lobón-Cerviá 2007). In stream-dwelling salmonids, body growth has a direct effect on competitive interactions (Peery et al. 2004) and indirect effects on several life history traits, such as age-at-maturity (e.g., Morita & Fukuwaka 2006) and egg (e.g., Koops et al. 2004) and gamete production (Jonsson et al. 1996). This clearly indicates density-dependent growth as one potential mechanism of population regulation at the adult stage (Vincenzi et al.

2008a). Both scramble and contest competition have been proposed as explanations for decreased growth rates with increasing population densities (Ward et al. 2007).

Studies investigating density-dependent growth in freshwater salmonids have typically focused on underyearlings, with the relationship between density and mean body size of year-classes following negative power curves (for a comprehensive review see Grant & Imre 2005). Minor variations in growth over high mean density, along with insufficient sample size of the data set, may also explain why density-dependent growth has gone undetected in populations at persistently high densities (Egglisshaw & Shackley 1977;

Mortensen 1977; Elliott 1994). So far, little attention has been devoted to density-dependent effects on body growth during the postrecruit phase in salmonid fishes. Davey et al. (2006) pointed out that a bias in the literature toward salmonid species which frequently engage in strong territorial competition as juveniles may be the cause of an underestimation of the prevalence of density-dependent growth in adult stream fish.

The detection of compensatory patterns such as density-dependent body growth can be affected by the spatial scale at which these patterns are investigated, that is, the scale at which mean density and mean body size are derived. Density-dependence should be estimated by averaging population numbers or densities over areas that are scaled appropriately to the movements of the individuals studied. Especially in the case of mobile organisms, study areas need to be large enough to detect the average density of conspecifics experienced by individuals. Ray & Hastings (1996) suggested as a rule of thumb that data should be scaled such that no more than 10% of individuals moves across its boundaries. Moreover, limited movement or dispersal can provide the conditions for the subdivision of a global population into several local populations with independent dynamics. In an interesting and influential study on brown trout, Jenkins et al. (1999) investigated the occurrence of density-dependent growth in underyearlings at different spatial scale, from 'segments' (5–31 m in length – riffles, run and pools) to 'sections' (340–500 m in length), either by manipulating densities in experimental settings or in the wild. Not surprisingly, the clearest evidence of the occurrence of density-dependent growth was provided by the experimental settings in which densities were artificially produced. Anyway, the pattern was also observed, although less clearly, with natural variations in density occurring in the wild. Jenkins et al. (1999) suggested that a sampling area needs to be at least 100 m<sup>2</sup> to capture the trout density experienced by the average individual over the preceding growth period. Moreover, the availability of food, such as invertebrate drift, is affected by individuals living upstream. Therefore, food local abundance may depend on trout density in a much larger area than that directly experienced by a trout. Another aspect potentially influencing the scale at which density-dependent growth may be detected is the mobility of organism, and it has been observed that trout may move over considerable distances (Gowan et al. 1994).

In a study on four marble trout (*Salmo marmoratus* Cuvier 1817) populations living in Slovenian streams (Gatsnik, Gorska, Huda and Zakojska), Vincenzi et al. (2008b) found a clear negative relationship between the mean age-specific body length of a year-class and total density of conspecifics experienced by the

individuals of the year-class during their first year of life. The variables of the density-dependent relationship were computed at the *whole stream* level. Data on mean length and density of the four populations were pooled together to increase sample size and to cover a wider range of densities. On the contrary, the studied streams are divided in sectors delimited by natural barriers generally restraining and in some cases preventing the upstream movement of marble trout. Limited movement and dispersal might provide the conditions for the establishment of independent population dynamics and trout in different sectors might experience different density. By averaging out lengths and densities at the *whole stream* level we might actually lose important information on density-dependent patterns at smaller scales.

Aim of this study was to investigate the relationship between density of marble trout during the first year of life and mean body size through the lifetime of year-classes at two spatial scales – the *sector* level (length and weight) and the *whole stream* level (only weight) – in order to derive insights on the scale at which density-dependent growth may be observed. Specifically, we explored: (i) the existence of a significant relationship between body size (both length and weight) and population density also when computing mean body size and density at the *sector* level; (ii) whether the presence of physical barriers preventing the upstream movement of fish may affect the strength of the density-dependent relationship.

### Material and methods

Study area, collection methods, sampling surveys and translocation methods for the creation of new populations have been described in detail elsewhere (Crivelli et al. 2000; Vincenzi et al. 2008a; b); therefore, only aspects relevant to this study are reported here along with some of the results presented in Vincenzi et al. (2008b).

### Species description and studied populations

Sexual maturation of marble trout is size-dependent; spawning occurs at a minimum body length of 200 mm and typically when females are 3+ (Vincenzi et al. 2008a). Egg production is positively related to female length and iteroparity is commonly observed (Vincenzi et al. 2008a). Spawning takes place in November–December whereas hatching occurs in March and emergence in May–June. Marble trout feed preferentially on invertebrates, with some evidence of cannibalism (Dusan Jesensek, pers. comm.).

Today, only seven remnant pure (less than 2% of foreign genes, Fumagalli et al. 2002) populations persist in the Soca and Idrijca river basins (Slovenia,

Crivelli et al. 2000), the Huda population being one of them. As part of a conservation plan started in 1993 (Crivelli et al. 2000), three new populations were created by stocking 1+ individuals raised in the fish farm in previously fishless streams (Zakojska, Gorska and Gatsnik). The populations of Gorska and Zakojska were created in 1996 by stocking 500 individuals aged 1+ in each stream while the population of Gatsnik was created in 1998 by stocking 599 marble trout aged 1+. Marble trout raised in the fish farm were introduced in headwater stretches located between impassable waterfalls (Table 1) and successfully reproduced within the streams. Marble trout is the only fish species within the headwaters of the four studied streams. The Gorska population was wiped out by a severe debris flood in October 2004 while the marble trout populations of Huda and Zakojska experienced a major drop in population size after severe floods in October 2004 and in September 2007, respectively. The four streams differ greatly in habitat features (Table 1), with Gorska and Zakojska divided in sectors separated by natural physical barriers (i.e., waterfalls) allowing only limited downstream movement of trout and thus called one-way streams. On the contrary, Gatsnik and Huda are two-way streams (Huda being steeper), as marble trout can move from sector to sector in either upstream and downstream direction (Table 1).

Data collection

Sampling surveys were performed every June on the whole length of the headwater stretches from 1997 to 2005 for Gorska, from 1997 to 2007 for Zakojska, from 1999 to 2007 for Gatsnik and from 2001 to 2007 for Huda, respectively. We electrofished every stream two times starting from downstream by using a gasoline-powered, portable backpack electrofishing unit, to produce a multiple-pass removal estimate of trout abundance using Microfish 3.0 (Van Deventer & Platts 1989). All captured fish aged  $\geq 1+$  were anaesthetised with benzocaine, measured for total length ( $L$ , to the nearest mm) and weight ( $W$ , g) and if sampled for the first time the adipose fin was removed and scales were taken for age assessment. Trout longer

than 115 mm ( $L$ ) were marked with Carlin tags (Institute of Freshwater Research, Sweden). Marble trout were returned live near the point of capture. Age was determined by tag examination or by reading scales if the individual was not tagged (first sampling or tag lost). Capture rates in the streams are higher than 80%. The small size of marble trout aged 0+ prevented their sampling in June and therefore they were not included in this study. Sex determination was not possible in June due to lack of gonad development. Maximum age observed for marble trout period in the studied streams was 8 years.

Statistical methods

The statistical analyses presented here were carried out only on marble trout hatched in the streams and were performed in four steps.

First, we investigated movement rate across sectors by computing over the entire sampling period the percentage of marble trout sampled at year  $t + 1$  in a sector different from the one where the fish was sampled at year  $t$ .

Second, differences in mean density across years among sectors were estimated for Gatsnik and Zakojska by fitting a linear mixed-effect model (Pinheiro & Bates, 2000) with year of sampling modelled as random effect.

Third, we investigated which explanatory variables better explain variations in mean age-specific body length and weight ( $\bar{L}_x, \bar{W}_x, x = 1 + \dots 5 +$ ) of marble trout year-classes at the *sector* level ( $\bar{L}_x^{sc}, \bar{W}_x^{sc}$ ) and at the *whole stream* level ( $\bar{L}_x^{ws}, \bar{W}_x^{ws}$ ). We did not investigate body size at ages  $> 5+$  as we lacked the necessary sample size. We assumed that marble trout spent their first of life in the sector where they were sampled for the first time.

$\bar{L}_x^{sc}$  and  $\bar{W}_x^{sc}$  were computed for each stream and sampling year  $t$  as the sector-specific mean length and weight of  $x$ -year-old trout ( $x = 1 + \dots 5 +$ ), respectively, where sc identifies the sector.  $\bar{L}_x^{ws}$  and  $\bar{W}_x^{ws}$  were computed for each stream and for each sampling year  $t$  as the stream-specific mean length and weight of  $x$ -year-old trout ( $x = 1 + \dots 5 +$ ) in the stream

Table 1. Main habitat features of the four studied streams.

Main features	Gatsnik	Gorska	Huda	Zakojska
Length (m)	2148	1032	338	1236
Total pool surface (m <sup>2</sup> )	2705	817	147	955
Number of sectors	6	11	2	6
Range and mean of sectors length (m)	260.0–516.76 (336.82)	35.2–136.22 (75.9)	90.82–149.64 (112.7)	113–228.14 (170.99)
Range and mean of pool area in sectors (m <sup>2</sup> )	229.1–585.9 (396.0)	26.69–135.35 (62.3)	102.9–149.8 (125.4)	29.8–202.3 (124.6)
Pool area as % of total surface	39.4	38	16	25.3
Altitude range (m.a.s.l.)	899–924	400–514	529–581	578–728
Stream type	Two-way	One-way	Two-way	One-way

In one-way streams marble trout can basically move only from upstream to downstream, while in two-way streams marble trout can move in either direction.

(i.e., along all sectors), respectively.  $\bar{L}_x^{ws}$  values have been already reported in Vincenzi et al. (2008b). Trout that moved from one sector to another were not used to compute  $\bar{L}_x^{ws}$  and  $\bar{W}_x^{ws}$ .

ANCOVAs were performed on the ln-transformed response variables  $\bar{L}_x^{sc}$  and  $\bar{W}_x^{sc}$  ( $x = 1 + \dots 5 +$ ) separately for Gatsnik and Zakojska (for only these two populations we had the minimum sample size for the statistical analyses). We chose as independent variables age, year, sector, the sector-specific density of all marble trout aged  $\geq 1+$  experienced by the individuals of a year-class during the first year of life (from here on referred to as  $\bar{D}_u^{sc}$ ) and the sector-specific density of marble trout when they are aged  $x$  ( $\bar{D}_x^{sc}$ ). Both  $\bar{D}_u^{sc}$  and  $\bar{D}_x^{sc}$  were ln-transformed in the ANCOVA model. We included  $\bar{D}_u^{sc}$  (ind m<sup>-2</sup>) as a candidate predictor of body growth through the lifetime as growth rates and morphological, physiological and behavioural traits in a number of species are triggered by early experience, nutritional and habitat conditions and then become relatively fixed (e.g., Schlichting & Pigliucci 1998; Bateson 2001). Moreover, Vincenzi et al. (2008b) found a significant relationship between  $\bar{D}_u^{ws}$  and  $\bar{L}_x^{ws}$  for all ages, while density after the first year of life of the cohort ( $\bar{D}_x^{ws}$ ) did not explain a significant part of the variability in  $\bar{L}_x^{ws}$ . Densities  $\bar{D}_u^{sc}$  and  $\bar{D}_u^{ws}$  of marble trout were computed by dividing the estimated number of marble trout aged  $\geq 1+$  living in a sector ( $\bar{D}_u^{sc}$ ) or in the whole stream ( $\bar{D}_u^{ws}$ ) during the first year of life by the overall pool area of the sector (for  $\bar{D}_u^{sc}$ ) or of the whole stream (for  $\bar{D}_u^{ws}$ ) in which the cohort lived. As marble trout live preferentially in pools, pool area offered the best quantification of in-stream habitat available for marble trout (Dusan Jesensek, pers. comm.). As sampling was performed once a year, density  $\bar{D}$  was computed as the mean of density of marble trout at year  $t - 1$  and at year  $t$ , where  $t$  is the year when the year-class was  $1+$  (for  $\bar{D}_u^{ws}$  and  $\bar{D}_u^{sc}$ ) or aged  $x$  (for  $\bar{D}_x^{sc}$ ).

Finally, where significant, we investigated the relationship between density  $\bar{D}$  (either  $\bar{D}_u$  or  $\bar{D}_x$ ) and the age-specific response variables  $\bar{L}_x$  and  $\bar{W}_x$  ( $x = 1 + \dots 5+$ ) either at the *sector* level (sc) and at the *whole stream* level (ws). Specifically, we fitted straight lines, in the form  $\bar{L}_x = a + b\bar{D}$  and  $\bar{W}_x = a + b\bar{D}$ , and negative power curves after logarithmic transformation, in the form  $\ln(\bar{L}_x) = \ln \alpha + \beta \ln \bar{D}$  and  $\ln(\bar{W}_x) = \ln \alpha + \beta \ln \bar{D}$ . The analysis at the *sector* level was carried out for each age class  $x$  by pooling together data on mean density (either  $\bar{D}_u^{sc}$  or  $\bar{D}_x^{sc}$ ) and mean body size (both  $\bar{L}_x^{sc}$  and  $\bar{W}_x^{sc}$ ) across years and sectors. As in Zakojska the surface of several pools is less than the minimum sampling area suggested by Jenkins et al. (1999) to capture the trout density actually experienced by an average individual over the preceding growth period,

we carried out the same analysis by using as independent variable the two-sector mean density, that is, the mean of the densities (either  $\bar{D}_u^{sc}$  or  $\bar{D}_x^{sc}$ ) estimated in the sector in which the cohort lived and in the sector upstream.

The analysis at the *whole stream* level was performed for each age class  $x$  by pooling together data on mean density (either  $\bar{D}_u^{ws}$  or  $\bar{D}_x^{ws}$ ) and mean body weight  $\bar{W}_x^{ws}$  across years and across the four studies populations. The effect of density on body length  $\bar{L}_x^{ws}$  at the whole stream level was already presented in Vincenzi et al. (2008b); the relationship was also reported in this work to facilitate the comparison with the new results obtained at the *sector* level.

Akaike information criterion (AIC) was used to explore which model form better fitted the observed pattern. AICs were calculated for the linear (AIC<sub>linear</sub>) and negative power (AIC<sub>power</sub>) model. Negative power model was assumed to be the best if AIC<sub>power</sub> - AIC<sub>linear</sub> < 2 (Motulsky & Christopoulos 2004).

The significance level  $\alpha$  for all statistical tests was set at 0.05. All statistical analyses were performed by using the software R (R Development Core Team, 2006).

## Results

A total of 6031, 442, 2021 and 277 marble trout hatched within the streams were sampled in Gatsnik, Gorska, Zakojska and Huda, respectively. Analysis of movement of marble trout showed a frequency of movement of individuals among sectors for all years of sampling combined of 10% in Gatsnik, 2.4% in Zakojska, 5.1% in Gorska and 10.6% in Huda, respectively. As expected, in Gatsnik and Huda trout moved both upstream and downstream whereas in Zakojska and Gorska only downstream movement was observed. Mean length and weight at age  $1+$  in sectors in Gatsnik and Zakojska are reported in Table 2, whereas densities estimated at the *sector* level and at the *whole stream* level in Gatsnik and Zakojska are showed in Fig. 1.

Significant differences in mean fish density among sectors were found in both Gatsnik and Zakojska (Gatsnik,  $F_{5,30} = 19.82$ ,  $P < 0.01$ ; Zakojska,  $F_{5,35} = 21.11$ ,  $P < 0.01$ ).

Besides the large effect of age, the two most important variables explaining a significant proportion of the overall variation in mean age-specific length  $\bar{L}_x^{sc}$  of year-classes at the *sector* level in Gatsnik and Zakojska were sector and trout density  $\bar{D}_u^{sc}$  experienced by the year-class during its first year of life (Table 3). On the contrary, population density at age  $x$   $\bar{D}_x^{sc}$  was not significant in both streams, while year-effect and the interaction between  $\bar{D}_u^{sc}$  and sector was significant only in Gatsnik.

Table 2. Mean density (ind m<sup>-2</sup>) in sectors in Gatsnik and Zakojska during the study period and mean individual length (mm) and weight (g) of year-classes at age 1+  $L_{1+}^{sc}$ .

Sector	Mean (±SD)	$\bar{L}_{1+}^{sc}$ (±SD)	$\bar{W}_{1+}^{sc}$ (±SD)
<i>Gatsnik</i>			
1	0.13 ± 0.07	119.5 ± 12.2	18.04 ± 5.79
2	0.57 ± 0.31	112.9 ± 12.8	15.18 ± 5.69
3	0.30 ± 0.16	113.2 ± 15.1	15.11 ± 6.22
4	0.63 ± 0.30	107.9 ± 12.0	12.94 ± 4.23
5	0.27 ± 0.14	105.3 ± 13.3	12.45 ± 4.43
6	0.30 ± 0.13	99.8 ± 9.2	10.65 ± 3.11
<i>Zakojska</i>			
1	0.70 ± 0.23	124.1 ± 5.0	19.72 ± 2.85
2	0.42 ± 0.13	113.6 ± 3.7	15.23 ± 1.74
3	0.20 ± 0.09	122.3 ± 16.2	19.59 ± 7.43
4	0.29 ± 0.09	114.2 ± 5.2	16.24 ± 1.73
5	0.46 ± 0.14	114.3 ± 11.8	16.13 ± 4.36
6	0.18 ± 0.05	117.6 ± 7.1	17.24 ± 3.78

Sector 6 is the most upstream sector in both streams.

Mean individual weight of year-classes at the *sector* level  $\bar{W}_x^{sc}$  was clearly related to age, sector, and density during the first year of life  $\bar{D}_u^{sc}$  in Gatsnik, whereas in Zakojska the significance level  $P$  for  $\bar{D}_u^{sc}$  was slightly above 0.05 (Table 3). In addition, in the case of weight as response variable, the sector density  $\bar{D}_x^{sc}$  experienced at age  $x$  did not explain a significant proportion of the variance in  $\bar{W}_x^{sc}$  in neither streams while the interaction between density during the first year of life  $\bar{D}_u^{sc}$  and sector was significant only in Gatsnik (Table 3). As for both length and weight  $\bar{D}_x^{sc}$  was not significant in the ANCOVAs, we performed the regression analyses by using early density  $\bar{D}_u^{sc}$  as predictor of body size.

At the *sector* level, in Gatsnik the mean individual length  $\bar{L}_x^{sc}$  of year-classes was negatively related to total density of marble trout aged  $\geq 1+$  during their first year of life  $\bar{D}_u^{sc}$  for all ages from 1+ to 5+ (Fig. 2c). In Zakojska, the relationship between  $\bar{L}_x^{sc}$  and  $\bar{D}_u^{sc}$  was significant only for age 2+, 3+ and 4+ (Fig. 2b).

In both Gatsnik and Zakojska, power curves provided a better fit than straight lines for each age.

No noticeable differences were observed in the statistical significance and coefficient of determination of the age-specific relationships in Zakojska when the independent variable was computed as the mean of the densities  $\bar{D}_u^{sc}$  in the sector in which the cohort lived and in the sector upstream.

At the *whole stream* level, the relationship between  $\bar{W}_x^{sc}$  and  $\bar{D}_u^{sc}$  was significant for all ages in Gatsnik and well explained by power curves (Fig. 3c), whereas in Zakojska the relationship was significant only for age 2+, 3+ and 4+ (Fig. 3b), with a low coefficient of determination (Table 4). At the *whole stream* level, the relationship between  $\bar{W}_x^{ws}$  and  $\bar{D}_u^{ws}$  was significant for all the ages from 1+ to 5+ (Fig. 3a). In addition, in this case, power curves provided a better fit than straight lines.

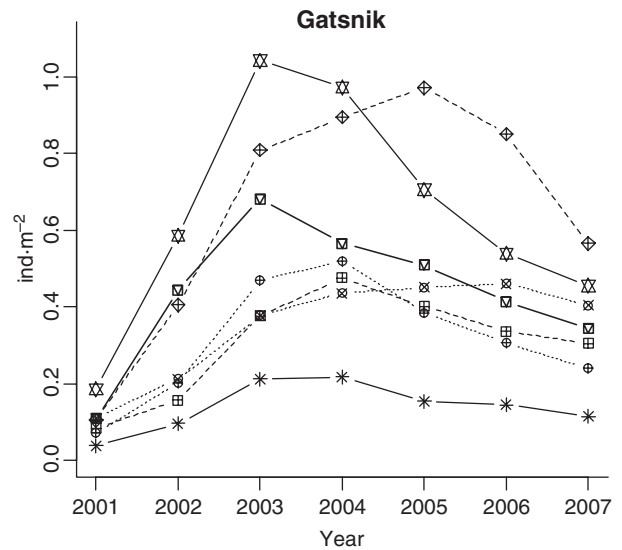
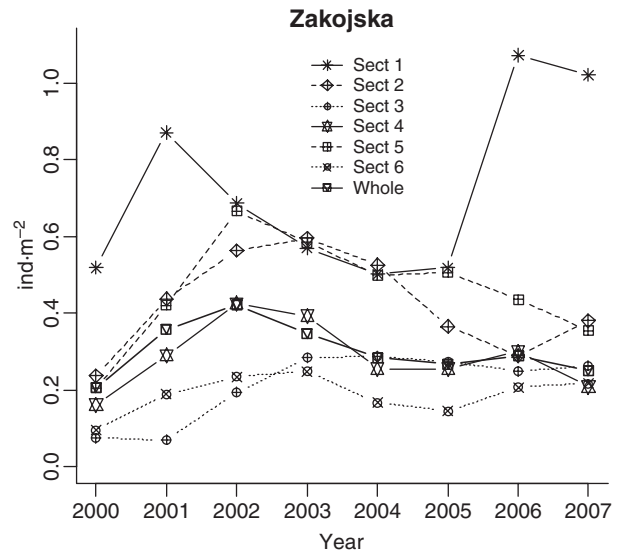


Fig. 1. Density of marble trout in ind. m<sup>-2</sup> at the *sector* level and at the *whole stream* level in Gatsnik and Zakojska.

### Discussion

In this study, we showed how the detection of the effects of total population density on body growth in marble trout populations living in streams divided in sectors may depend on the spatial scale at which the pattern is investigated. Population density  $\bar{D}_u^{ws}$  of marble trout during the first year of life of year-classes estimated at the *whole stream* level has a clear effect through trout lifetime on mean individual weight  $\bar{W}_x^{sc}$  (Fig. 3a and Table 4) of year-classes. In a previous work, Vincenzi et al. (2008b) found that also the relationship between mean individual length of year-classes  $\bar{L}_x^{ws}$  and density during the first year of life  $\bar{D}_u^{ws}$  estimated by pooling together the four stream-specific data sets was significant for all ages (Fig. 2a and Table 4).

## Density-dependent growth at two spatial scales

Table 3. ANCOVAs of the effects of age, year and, sector, ln-transformed density of marble trout aged  $\geq 1+$  during the first year of life ( $\bar{D}_u^{sc}$ ) and ln-transformed density of marble trout aged  $\geq 1+$  ( $\bar{D}_x^{sc}$ ) on ln-transformed mean individual length and weight of year-classes at the *sector* level in Gatsnik and Zakojska.

Length	Gatsnik						Zakojska					
	$R^2 = 0.98$						$R^2 = 0.96$					
Variable	d.f.	Partial SS	MS	F	P	Partial $R^2$	d.f.	Partial SS	MS	F	P	Partial $R^2$
$\bar{D}_u^{sc}$ (F + HF)	6	0.71	0.11	46.07	< 0.01	0.04	6	0.06	0.01	2.32	<0.05	0.003
$\bar{D}_x^{sc}$	1	0.01	0.01	3.54	0.06	0.0005	1	0.01	0.01	1.56	0.21	0.0001
Age	5	7.99	1.60	620.83	<0.01	0.43	5	13.94	2.79	638.92	<0.01	0.70
Year	6	0.28	0.01	4.78	<0.01	0.004	7	0.06	0.01	2.43	0.07	0.002
Sector(F + HF)	10	0.28	0.03	10.89	<0.01	0.01	10	0.48	0.05	11.00	<0.01	0.02
$\bar{D}_u^{sc} \times \text{sector}$ (F + HF)	5	0.04	0.008	3.21	<0.01	0.002	5	0.03	0.01	1.47	0.2	0.002
Weight	$R^2 = 0.98$						$R^2 = 0.96$					
$\bar{D}_u^{sc}$ (F + HF)	6	05.57	0.93	37.66	<0.01	0.04	6	0.53	0.09	2.07	0.06	0.003
$\bar{D}_x^{sc}$	1	0.07	0.07	2.88	0.09	0.0004	1	0.009	0.009	1.56	0.21	0.00005
Age	5	69.58	13.92	564.82	<0.01	0.44	5	120.82	24.16	638.92	<0.01	0.69
Year	6	1.07	0.18	7.22	<0.01	0.007	7	0.88	0.12	2.94	<0.01	0.005
Sector(F + HF)	10	1.94	0.19	7.88	<0.01	0.01	10	4.5	0.45	10.62	<0.01	0.026
$\bar{D}_u^{sc} \times \text{sector}$ (F + HF)	5	0.32	0.06	2.58	<0.05	0.002	5	0.39	0.08	1.85	0.11	0.002

F + HF means Factor + Higher Order Factors. Partial  $R^2$  for predictors are also reported.

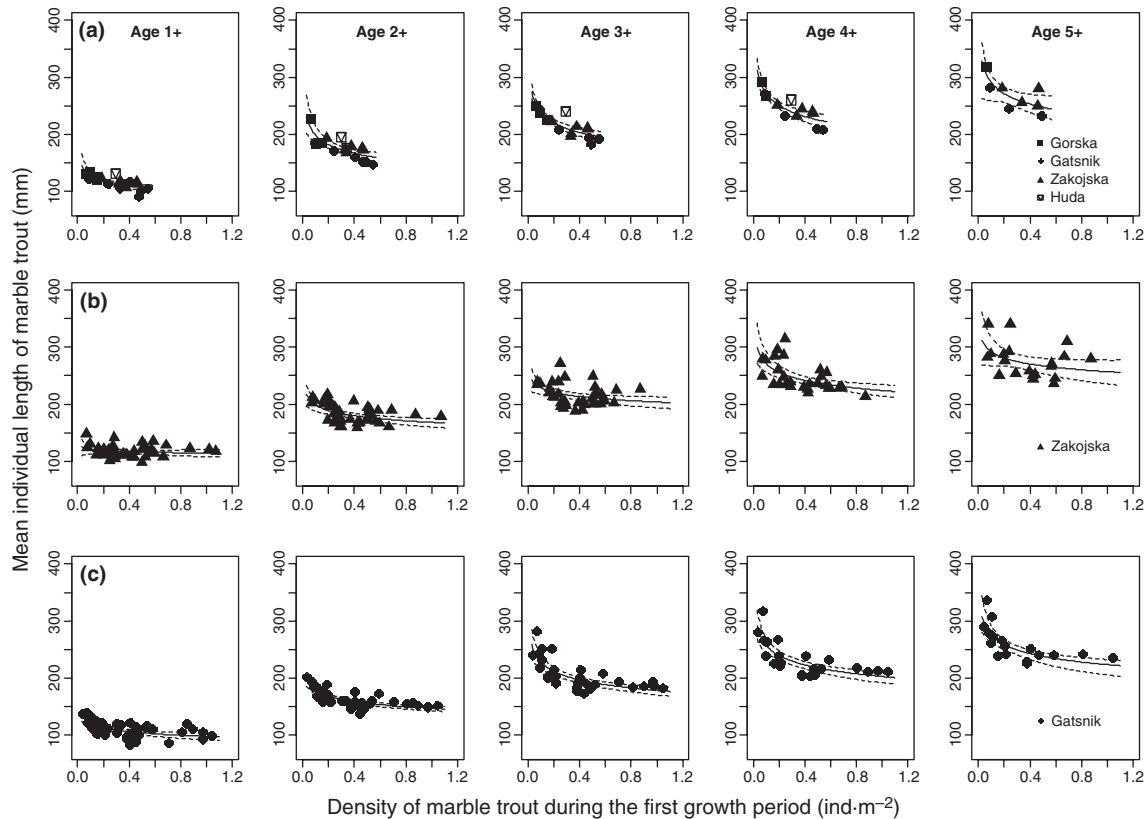


Fig. 2. (a) Mean body length of year-classes  $\bar{L}_x^{ws}$  versus density at the *whole stream* level  $\bar{D}_u^{ws}$  for the pooled data set of the four populations (already reported in Vincenzi et al. 2008b). (b and c) Mean body length of marble trout year-classes  $\bar{L}_x^{sc}$  versus density at the *sector* level of individuals aged  $\geq 1+$  during the first year of life  $\bar{D}_u^{sc}$  for the populations of Zakojska (b) and Gatsnik (c). For (b) and (c), each point represent data on age-specific trout length and density from different sectors. Negative power curves along with nonparametric bootstrap 95% confidence intervals (2000 replicates) are reported for each age.

As expected, movement across sectors was limited, with movement rates higher in the two-way streams (Gatsnik and Huda). Given the low movement rates,

the assumption that marble trout lived the first year of life where they were sampled at age 1+ seems acceptable.

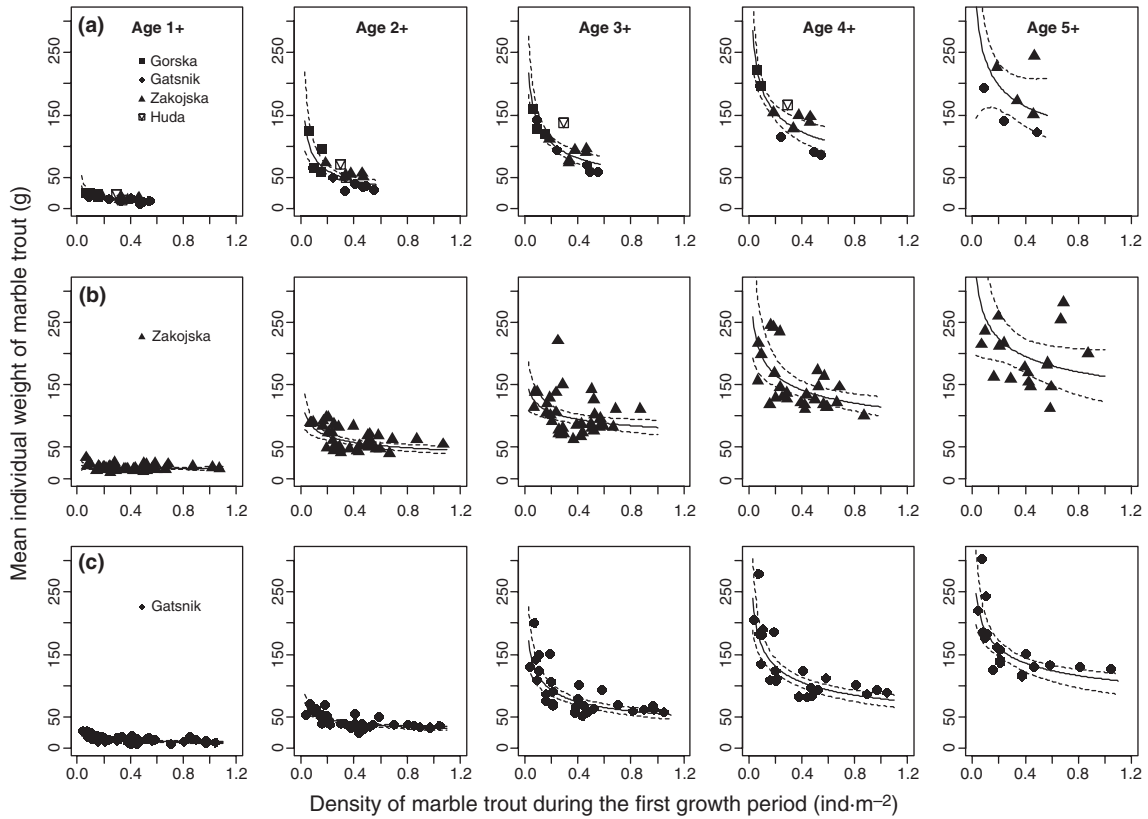


Fig. 3. (a) Mean body weight of year-classes  $\bar{W}_x^{ws}$  versus density at the whole stream level  $\bar{D}_u^{ws}$  for the pooled data set. (b and c) Mean body weight of marble trout year-classes  $\bar{W}_x^{sc}$  versus density at the sector level of individuals aged  $\geq 1+$  during the first year of life  $\bar{D}_u^{sc}$  for the populations of Zakojska (b) and Gatsnik (c). For (b) and (c), each point represents data on age-specific trout weight and density from different sectors. Negative power curves along with nonparametric bootstrap 95% confidence intervals (2000 replicates) are reported for each age.

Table 4. Parameters values ( $\pm$ SE) of the models linking density during the first year of life of the year-class at the sector level  $\bar{D}_u^{sc}$  and at the whole stream level  $\bar{D}_u^{ws}$  to mean length and weight of year-classes, in the form  $\ln(\bar{L}_x^{sc}) = \ln \alpha + \beta \ln \bar{D}_u^{sc}$  and  $\ln(\bar{W}_x^{sc}) = \ln \alpha + \beta \ln \bar{D}_u^{sc}$  at the sector level,  $\ln(\bar{L}_x^{ws}) = \ln \alpha + \beta \ln \bar{D}_u^{ws}$  and  $\ln(\bar{W}_x^{ws}) = \ln \alpha + \beta \ln \bar{D}_u^{ws}$  at the whole stream level.

	Sector level								Whole stream level			
	Gatsnik				Zakojska				Pooled			
	Length											
Age	$\ln \alpha$	$\beta$	$P$	$R^2$	$\ln \alpha$	$\beta$	$P$	$R^2$	$\ln \alpha$	$\beta$	$P$	$R^2$
1 +	4.58 $\pm$ 0.03	-0.09 $\pm$ 0.02	<0.01	0.34	4.73 $\pm$ 0.02	-0.03 $\pm$ 0.02	0.21	0.01	4.59 $\pm$ 0.03	-0.11 $\pm$ 0.02	<0.01	0.54
2 +	4.99 $\pm$ 0.02	-0.08 $\pm$ 0.01	<0.01	0.58	5.12 $\pm$ 0.03	-0.07 $\pm$ 0.02	<0.01	0.24	4.99 $\pm$ 0.03	-0.12 $\pm$ 0.01	<0.01	0.63
3 +	5.18 $\pm$ 0.02	-0.10 $\pm$ 0.02	<0.01	0.57	5.32 $\pm$ 0.03	-0.05 $\pm$ 0.02	<0.05	0.10	5.19 $\pm$ 0.02	-0.12 $\pm$ 0.02	<0.01	0.82
4 +	5.31 $\pm$ 0.03	-0.10 $\pm$ 0.01	<0.01	0.63	5.41 $\pm$ 0.03	-0.08 $\pm$ 0.02	<0.01	0.30	5.33 $\pm$ 0.03	-0.12 $\pm$ 0.01	<0.01	0.78
5 +	5.4 $\pm$ 0.35	-0.09 $\pm$ 0.02	<0.01	0.54	5.55 $\pm$ 0.04	-0.05 $\pm$ 0.03	0.08	0.11	5.44 $\pm$ 0.06	-0.10 $\pm$ 0.02	<0.01	0.51
	Weight											
1 +	2.23 $\pm$ 0.09	-0.30 $\pm$ 0.06	<0.01	0.35	2.74 $\pm$ 0.07	-0.07 $\pm$ 0.06	0.19	0.02	2.28 $\pm$ 0.11	-0.37 $\pm$ 0.07	<0.01	0.53
2 +	3.46 $\pm$ 0.05	-0.23 $\pm$ 0.04	<0.01	0.53	3.84 $\pm$ 0.08	-0.23 $\pm$ 0.06	<0.01	0.25	3.40 $\pm$ 0.13	-0.44 $\pm$ 0.09	<0.01	0.55
3 +	4.01 $\pm$ 0.07	-0.32 $\pm$ 0.05	<0.01	0.59	4.40 $\pm$ 0.09	-0.16 $\pm$ 0.07	<0.05	0.10	4.05 $\pm$ 0.11	-0.38 $\pm$ 0.07	<0.01	0.67
4 +	4.37 $\pm$ 0.07	-0.31 $\pm$ 0.05	<0.01	0.66	4.74 $\pm$ 0.10	-0.23 $\pm$ 0.08	<0.01	0.24	4.51 $\pm$ 0.12	-0.32 $\pm$ 0.07	<0.01	0.62
5 +	4.70 $\pm$ 0.08	-0.23 $\pm$ 0.05	<0.01	0.58	5.09 $\pm$ 0.14	-0.20 $\pm$ 0.10	0.06	0.13	4.85 $\pm$ 0.22	-0.27 $\pm$ 0.13	<0.01	0.30

Model parameters relative to  $\bar{L}_x^{ws}$  have already been reported in Vincenzi et al. (2008b).

Our analysis showed that variability in age-specific mean individual length  $\bar{L}_x^{sc}$  and weight  $\bar{W}_x^{sc}$  of year-classes at the sector level is partially explained by

sector-specific population density and by sector- and year-effects (Table 3). In Gatsnik, the interaction between sector and  $\bar{D}_u^{sc}$  was significant for both  $\bar{L}_x^{sc}$

and  $\bar{W}_x^{\text{sc}}$  and this means that sector-effect is dependent on sector-specific density during the first year of life. Density during the first year of life does seem to influence the body growth of marble trout. The result seem to support that body growth trajectories through the lifetime are heavily determined early in life, a carry-over effect of early density on body growth at subsequent ages.

The observed relationship between total density and growth of marble trout can have alternative explanations: it can be either a direct effect of total population density in the newly recruited cohort, that is, inter-cohort competition, or – if density were proportional to the spawning stock – the effect of intra-cohort competition for resources among underyearlings. In fact, in the latter case, the negative relation between body size growth of the newly recruited cohort and population densities of older cohorts should be interpreted as an indirect effect mediated by overall egg production. As underyearlings were not sampled in these streams, there is no field data to directly test these hypotheses. Yet, in Vincenzi et al. (2007, 2008a) we showed that density of underyearlings is not correlated neither with total density of marble trout nor with spawner density, as egg production is size-dependent and female size is density-dependent. Moreover, density-dependent inter-cohort competition in *S. trutta* and its effect on body growth rates were confirmed by Nordwall et al. (2001) and Kaspersson & Höjesjö (2009). Therefore, while further investigations are needed, we are inclined to believe that reduced growth rates result from increased intensity of inter-cohort competition.

The relationship between total population density at the *sector* level during the first year of life  $\bar{D}_u^{\text{sc}}$  and age-specific body size was stronger for both length  $\bar{L}_x^{\text{sc}}$  and weight  $\bar{W}_x^{\text{sc}}$  in Gatsnik, a stream in which movement across sectors is possible in either direction, than in Zakojska, where upstream movement is basically prevented by the presence of waterfalls (Figs 2 and 3; Table 4). This was surprising, as we expected that the effect of density at the *sector* level would be better detectable and stronger in the one-way stream in which waterfalls limiting movement may define the boundaries of local population dynamics. On the contrary, pool surface in sectors in Gatsnik is noticeably greater than in Zakojska (Tab. I); as a consequence, it could be argued that in Zakojska the minimum area to capture the average trout density experienced by an individual was not represented by sectors, but possibly at a larger scale. Jenkins et al. (1999) suggested 100 m<sup>2</sup> as minimum sampling area for brown trout. Nevertheless, even by using as a predictor of body size the mean of population density in two sectors (the one in which the year-class lived and the sector upstream) the statistical significance of the relationship did not improve.

Overall, the best evidence of density-dependent growth was offered by the analysis at the *whole stream* level using the pooled data set (Table 4), although the population of Huda was a clear outlier for both mean individual length (Fig. 2a) and weight (Fig. 3a) of year-classes, with mean size (either length and weight) consistently greater in Huda at any population density  $\bar{D}_u^{\text{ws}}$ . Further studies and more years of data are necessary in order to understand which factors are responsible of the observed differences.

In Gatsnik, the strength of the density–length relationship at the *sector* level (i.e., the slope of the power curves) was very similar to that observed at the *whole stream* level by using the pooled dataset, whereas differences were greater when the response variable was mean individual weight of year-classes. The density–weight relationship was stronger at the *whole stream* level with the pooled dataset than at the *sector level* in Gatsnik (Table 4). Our results showed that the relationship between density and body size growth was fairly weak when marble trout were 1+, both at the *whole stream* level and at the *sector* level, which may imply that body size at age 1+ also depends on other factors, such as the availability of suitable micro-habitat.

The results here presented have several implications. First, the detection of density-dependent growth may depend on the spatial scale at which the pattern is investigated. The appropriate spatial scale is likely to be related to the species and its ecology and the physical features of the stream. In the specific case of marble trout, as sectors of a stream may be characterised by mean density and trend that are different from that observed at the whole stream level (Fig. 1), it is seems reasonable that, whenever possible, density–dependent relationships are also tested by using data at the sector level. In addition to spatial scale, habitat quality is likely to be responsible for the occurrence of growth-density patterns. In an interesting study on density-dependent growth in stream-living brown trout in Rio Chaballos (Spain), Lobón-Cervía (2005) found that the interactions between body size and density occurred at a site scale (60–80 m in length) and varied in nature among sited to the extent that the density-dependent patterns were site-specific. Lobón-Cervía (2005) also reported that the specific life stage, ranges of density upon which density operated, and the relative importance of intra- and inter-cohort density varied greatly among sites and revealed a different operation of density depending on habitat quality. This led Lobón-Cervía (2005) to suggest that spatio-temporal variations in space suitable for sized individuals are the immediate factors responsible for the site-specific growth-density patterns. These findings deserve future investigations also for marble trout.

Second, limited movement of individuals across the boundaries of a sector may not be sufficient for the



establishment of independent population dynamics. In the case of Zakojska, contrarily to what was expected given the low movement rates of individuals, sectors may not identify local populations with independent population dynamics, but this might also depend on the limited pool surface in sectors. On the contrary, the relationship between mean individual length and weight of year-classes and density during the first year of life was clear in Gatsnik, a two-way stream with higher movement of marble trout across sectors.

Third, negative power curves always provided a better fit of the observed pattern than a linear regression. These results are in agreement with those of Jenkins et al. (1999) and Lobón-Cerviá (2007) for *S. trutta* and Imre et al. (2005) for *S. salar*, who hypothesised that body size of underyearlings follows a negative power curve in relation to fish density. Because of the shape of the relationship, large increments in body size are expected when the population drops at low densities.

The issues presented here are of fundamental importance for a better understanding of the role of density-dependent body growth in terms of population dynamics and resilience to the effects of catastrophic events, such as floods, droughts and landslides. In fact, a negative correlation between population abundance and individual growth that persists from the juvenile to the adult stage combined with a positive correlation between adult body size and reproductive output constitutes a compensatory mechanism for regulating recruitment (Jenkins et al. 1999). A simulation analysis was performed by using a data-driven individual based model of marble trout accounting for both density-dependent early survival and individual growth and the effects of autumnal severe flood events. The results of the simulation analysis suggested a potentially powerful role of density-dependent individual growth for compensatory recruitment (Vincenzi et al. 2008a). Given the fundamental importance of body growth of marble trout for the population dynamics, further studies are needed to identify the scale at which density-dependent growth operates, particularly in streams in which movement of individuals is constrained by natural barriers.

### Acknowledgements

We thank Fondation Sansouire and the Angling Association of Tolmin for funding this study. All the people who have participated each year to the fieldwork are warmly thanked. The author is also grateful to three anonymous referees for insightful and constructive suggestions.

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