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Letter

Total population density during the first year of life as a major determinant of lifetime body-length trajectory in marble trout

Abstract – The conditions experienced early in life can strongly influence life-history trajectories in a variety of animal species. Here, we use data from four isolated populations of the endangered stream-dwelling salmonid marble trout (*Salmo marmoratus* Cuvier 1817) living in the Soca and Idrijca river basins (Slovenia) to explore the influence of the total density experienced during and after the first year of life by marble trout year-classes on body length of marble trout through the lifetime. Analyses were performed by pooling together the stream-specific datasets to cover a wider range of densities. Mean body length of marble trout year-classes through the lifetime (from age 1+ to 5+) was negatively related to total density of marble trout during the first year of life. The relationship between density during the first growth period and body length through the lifetime was well described by negative power curves. Total population density after the first year of life was not correlated with body length, thus suggesting that body growth trajectories are heavily determined early in life. Given size-dependent sexual maturity and egg production in marble trout, the relationship between density early in life and lifetime individual growth may have strong implications in terms of population dynamics and regulation of population size.

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Introduction

The investigation of density-dependent individual growth in freshwater salmonids has received considerable attention in the last years and there is now a general consensus on its occurrence in a number of salmonid species (e.g., for brown trout, Crisp 1993; Jenkins et al. 1999; Lobón-Cerviá 2005, 2007; for Atlantic Salmon, Imre et al. 2005; for a meta-analysis on salmon and trout populations see Grant & Imre 2005). Empirical studies have shown that the relationship between average body growth of underyearlings and population density in stream-dwelling salmon and trout populations is well described by negative power curves (e.g., Jenkins et al. 1999; Imre et al. 2005; Lobón-Cerviá 2007). Based on the characteristic shape of the relationship, Grant & Imre (2005) asserted that density-dependent individual growth is determined by exploitative competition for a renewable resource, such as stream drift. On the contrary, Ward et al. (2007) showed that also competition for space can yield a concave density–growth relationship. Hence, a definitive answer on whether the observed pattern is due to exploitative or interference competition or a combination of the two is still lacking. Numerous studies have focused on processes occurring in larval and post-larval young-of-the-year (YOY) stages in salmonids. Conversely, little attention has been devoted to the investigation of how and to what extent the effects of density on growth at the juvenile stage persist through lifetime. There is increasing evidence that the conditions experienced early in life can strongly influence life-history trajectories in a variety of animal species (e.g., Schlichting & Pigliucci

1998). For instance, poor environment early in life can result in smaller adult size and in reduced lifetime fitness of individuals (Taborsky 2006). Early experience commonly influences growth, which may affect subsequent age and size-at-maturity if the effects of early experience persist through lifetime (Fleming et al. 1997). Lobón-Cerviá et al. (1997) found that the number of eggs produced by females aged 1+ was influenced by early growth in a brown trout living in the Esva River (Spain).

In stream-dwelling salmonids, the effects of body growth on several life history traits, such as age-at-maturity (e.g., Morita & Fukuwaka 2006) and egg production (e.g., Koops et al. 2004), clearly indicate density-dependent individual growth as one potential mechanism of population regulation. In fact, a negative correlation between adult abundance and juvenile growth that persists through to the adult stage combined with a positive correlation between adult body size and fecundity constitutes a compensatory mechanism for regulating recruitment (Jenkins et al. 1999). As a consequence, the degree to which early conditions influence lifetime growth is of particular interest in terms of population dynamics and persistence of freshwater salmonids.

Here, we explore the implications of the density experienced during and after the first year of life on the mean body length of year-classes through lifetime in four isolated populations (Zakojska, Gorska, Gatsnik and Huda Grapa) of the stream-dwelling salmonid marble trout (*Salmo marmoratus* Cuvier 1817) living in Slovenia. Some preliminary evidences of a contribution of early environment on growth of marble trout have been reported by Vincenzi et al. (2007b).

Materials and methods

Full details of study area, sampling surveys and translocation methods have been provided elsewhere (Crivelli et al. 2000; Vincenzi et al. 2007a,b; Vincenzi et al. 2008a). Therefore, only the aspects relevant to this study are reported here.

Salmo marmoratus is a freshwater salmonid inhabiting streams with summer temperature <14 °C and winter temperature ranging between 0 and 5 °C. In the studied streams, maximum length and weight of marble trout recorded were 396 mm and 768 g,

respectively. Maximum age for marble trout is 6+ with sexual maturation generally reached at 2+ and 3+ for males and females, respectively. Sexual maturation is size-dependent; spawning occurs at a minimum body length of 200 mm (Vincenzi et al. 2008a) and egg production is positively related to female length (Vincenzi et al. 2008a). Iteroparity is commonly observed in marble trout (Vincenzi et al. 2007a). Spawning takes place in November–December while hatching occurs in March and emergence in May–June. Today, only seven remnant pure (<2% of foreign genes, Fumagalli et al. 2002) populations persist in the Soca and Idrijca river basins (Slovenia, Crivelli et al. 2000). The marble trout population of Huda Grapa is one of the seven remnant pure populations of marble trout and has been viable since thousands of years (A. J. Crivelli, personal communications) despite the low population size (28–74 individuals ≥ 1+ in the study period). As part of a conservation plan launched 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 in each stream while the population of Gatsnik was created in 1998 by stocking 599 marble trout. Stocking material was 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.

Sampling surveys were performed every June on the whole length of the 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 Grapa. Main features of the four studied streams are reported in Table 1. 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 ≥1+ and with a minimum size of 115 mm (*L*) were anaesthetized with benzocaine, marked with Carlin tags (Institute of Freshwater Research, Sweden), 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

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

Main features	Gatsnik	Zakojska	Gorska	Huda Grapa
Length (m)	2021	1238	845	338
Wetted surface (m^2)	6035	3544	1805	914
Pool surface (m^2) (% of total surface)	2375 (39.4%)	895 (25.3%)	685 (38%)	375 (41%)
Mean summer temperature (*n* = 6)	12.74 ± 1.54	13.67 ± 0.58	13.39 ± 0.49	12.77 ± 0.94
Altitude range (m.a.s.l.)	899–924	578–728	400–514	557–583

Each studied stretch is located between two impassable waterfalls.

and scales were taken for age assessment. Then, marble trout were returned live near the point of capture. Age was determined by tag examination. 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 gonads development. A total of 6031, 442, 2021 and 277 marble trout hatched in the streams aged ≥1+ were sampled in Gatsnik, Gorska, Zakojska and Huda Grapa, respectively.

The statistical analyses presented here were carried out only on marble trout hatched in the streams, as stocking material is likely to exhibit growth patterns quite different from marble trout hatched in the streams. All statistical analyses were performed by pooling together the four stream-specific datasets (Gatsnik, Gorska, Huda and Zakojska) to cover a wider range of densities. We used only data from year-classes with more than five individuals. Accordingly, in our analyses we included a total of 21 cohorts (i.e., year-classes) aged 1+, 18 aged 2+, 15 aged 3+, 12 aged 4+ and 8 cohorts aged 5+.

We analysed the relationship between mean body length at age x ($\overline{L}_x$, $x = 1+,\ldots, 5+$) of year-classes and total density of marble trout D_u during the first growth period. Total density of marble trout was computed by dividing the total number of marble trout sampled aged ≥ 1+ (for the three experimental streams this includes also the stocking material) for the overall pool area, as it offered the best quantification of instream habitat available for marble trout. Although riffles are generally the most productive waters, the ratio between total pool area and stream surface is similar in all streams (Table 1). D_u was computed as the mean of total density of marble trout at year $t - 1$ and at year t, where t is the year when the year-class was 1+. The relationship between $\overline{L}_x$ and D_u was tested separately for each age x from 1+ to 5+ by using either ordinary least-squares regression and a power curve after logarithmic transformation, in the form $\ln(\overline{L}_x) = \ln\alpha + \beta\ln D_u + \varepsilon$. We used the Akaike Information Criterion (AIC, Motulsky & Christopoulos 2004) to explore which model form was a better descriptor of the length–density relationship; the model with the smallest AIC value was considered to offer a markedly better fit if $AIC_{power} - AIC_{linear} \geq |2|$ (Motulsky & Christopoulos 2004).

Then, we tested whether the total density of trout when marble trout cohort was aged x (D_x) was able to explain the residuals of the relationship between $\overline{L}_x$ and D_u. D_x was computed as the mean of total density of marble trout at year $t_x - 1$ and at year t_x, where t_x is the year when the year-class was aged x. The analysis was performed separately for each age x from 2+ to 5+. The analysis of residuals could not be performed for $\overline{L}_{1+}$, as in this case D_x equals D_u.

Pearson's r was used to test the correlation between $\overline{L}_{1+}$ and $\overline{L}_{2+,\ldots,5+}$ after log-transformation of variables. Assumptions of normality were assessed by visual inspection of residuals. Due to the low sample size, the significance level α was set at the 0.01 level.

Results

The mean individual length L_x of year-classes through lifetime was negatively related with total density of
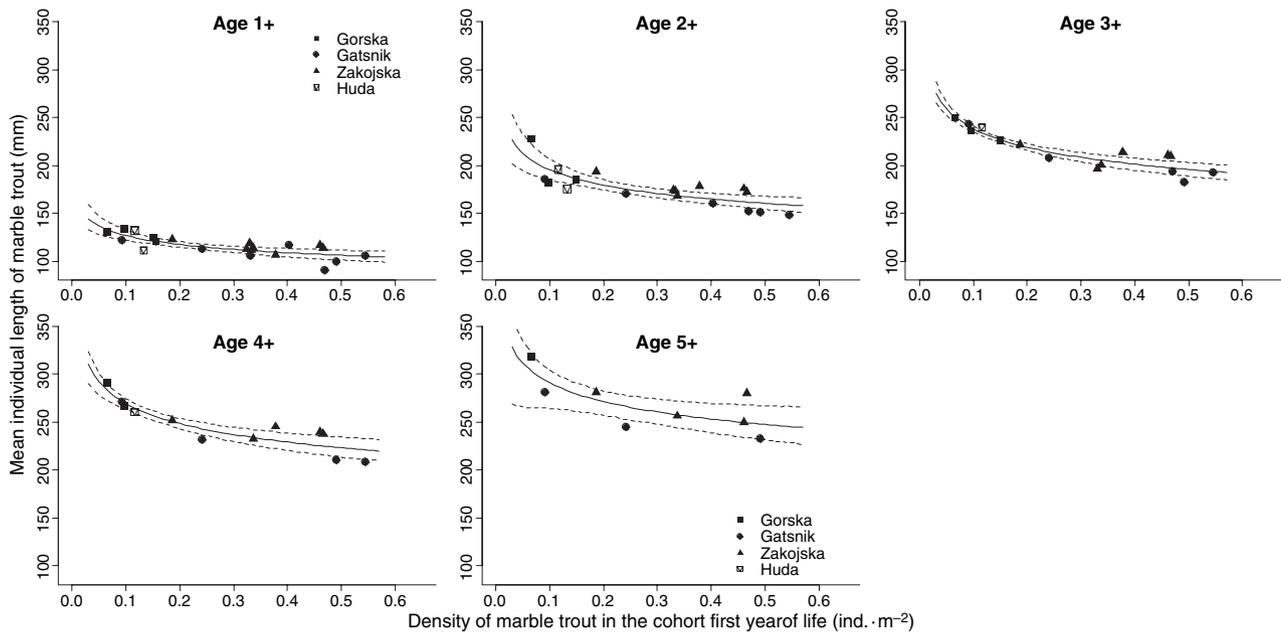
Fig. 1. Mean body length of marble trout year-classes $\overline{L}_x$ (mm) versus total density of individuals aged ≥1+ during the first year of life D_u (ind. · m⁻²). Negative power curves along with non-parametric bootstrap 95% confidence intervals (2000 replicates) are reported for each age.

Table 2. Parameters values (±SE) of model linking density during the first year of life of the cohort D_u (ind.·m^{-2}) to mean individual length $\overline{L}_x$ ($x = 1+,...,5+$) of marble trout cohorts trough lifetime in the form $\ln(\overline{L}_x) = \ln\alpha + \beta\ln D_u + \varepsilon$.

Age	Model results		
	$\ln \alpha$	β	R^2_{adj}
1+	4.59 ± 0.03	−0.11 ± 0.02	0.54
2+	4.99 ± 0.03	−0.12 ± 0.02	0.63
3+	5.19 ± 0.02	−0.12 ± 0.01	0.82
4+	5.33 ± 0.03	−0.12 ± 0.02	0.78
5+	5.44 ± 0.06	−0.10 ± 0.03	0.51

$P < 0.01$ for all ages.

marble trout during the first year of life (Fig. 1), the relationship being significant for all ages from 1+ to 5+ (Table 2). The power curve provided a better fit of the density-dependent pattern with respect to the straight line (AIC$_{power}$ − AIC$_{linear}$ < −2 for all ages). The density of marble trout D_x did not explain a significant proportion of the variance of $\overline{L}_x$ not already explained by D_u ($P > 0.01$ for all ages).

$\overline{L}_{1+}$ was positively correlated with $\overline{L}_{2+,...,5+}$ (age 2+: $r = 0.80$, $P < 0.01$; age 3+: $r = 0.73$, $P < 0.01$; age 4+: $r = 0.80$, $P < 0.01$, age 5+: $r = 0.75$, $P < 0.01$).

Discussion

Our results suggest a strong role of total density of marble trout aged ≥1+ during the first year of life in determining the mean individual length of year-classes through the lifetime. The relationship was well described by negative power curves (Fig. 1). Moreover, mean individual length of 1+ year-classes was positively correlated with individual length at subsequent ages. These results support the hypothesis that lifetime body-length trajectories are heavily determined early in life. On the contrary, at least in the range of densities observed in the marble trout populations studied here, total density after the first year of life does not seem to influence the body growth trajectories of marble trout year-classes. It is known that early growth and development can influence the size of organism throughout life (Arendt 2000) and that early growth may cause irreversible changes to the metabolism of individuals (Desai & Hales 1997). Growth trajectories may be triggered initially by nutritional and/or habitat conditions and then become relatively fixed, as shown for a number of morphological, physiological and behavioural traits (e.g., Bateson 2001). Low growth rates at the juvenile stages may be thus viewed as a phenotypic response sensitive to environmental conditions. Rapid growth of adults has been indeed observed in freshwater salmonids especially after severe flood events drastically reducing population density (Roghair et al.

2002). Given the phenotypic plasticity commonly observed in salmonids, it seems there is potential for catch-up growth rate in case of drastic reduction of population size, which was not observed in our analyses. The long-lasting effects of early environment on lifetime body-growth trajectories may have important implications in terms of population dynamics. As in freshwater salmonids sexual maturation is generally size-dependent and egg production is positively related to female length, the density of individuals during the first year of life is likely to influence the recruitment dynamics of marble trout. In addition, density-dependent first-year survival was found in marble trout populations living in Slovenian streams (Vincenzi et al. 2007a) while survival rates of marble trout ≥1+ were both density- and size-independent (Vincenzi et al. 2008). It is likely that both density-dependent first-year survival and density-dependent growth operate in the regulation of population size, with the size-dependent fecundity of year-classes influenced by population density 3–4 years before sexual maturation, as marble trout females first spawn at 3+ or 4+ depending on body length (Vincenzi et al. 2007b). Density-dependent body growth rates early in life can thus affect the reproductive performance of marble trout during the entire life-span. Moreover, density-dependent body growth may also enhance population recovery and reduce extinction risk in salmonid populations in a variable environment subject to disturbance events (Jenkins et al. 1999; Vincenzi et al. 2008b).

Despite further confirmations are needed, the results presented here clearly indicate a strong influence of early density on individual growth of marble trout through lifetime and also suggest important implications of this pattern in terms of population dynamics of marble trout living in the study area (Vincenzi et al. 2008b).

Acknowledgements

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