

Early survival of marble trout *Salmo marmoratus*: evidence for density dependence?

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Abstract –The role of endogenous and exogenous factors in regulating population dynamics of freshwater salmonids is still a matter of debate. The aim of the present work was to assess the relative importance of density-dependent and -independent factors in determining the survival of marble trout (*Salmo marmoratus*) yearlings in two populations living in Slovenian streams (Zakojska and Gorska). The investigation was performed by combining a classical life table analysis with Monte Carlo simulation. Size-dependent fecundity was estimated by stripping wild adults in the fish farm. A significant positive relationship was found between length of marble trout females and the number of eggs produced. Egg density was the major determinant of survival from eggs to age 1+ (σ_0) in both streams. Residuals of the relationship between σ_0 and egg density were positively correlated with rainfall only in Zakojska, probably because, within a certain range, more intense rainfalls increases stream flow and, consequently, suitable habitat for trout. Our study shows how density-dependent and environmental factors can interact to determine the survival of marble trout during the first year of life.

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Key words: density-dependent survival; marble trout; *Salmo marmoratus*; population dynamics; endogenous versus exogenous factors

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Introduction

The assessment of the importance of density-dependent processes regulating recruitment and population size in stream-living salmonids has been argument of strong debates in the last years (Jenkins et al. 1999, Milner et al. 2003; Lobón-Cervía & Rincón 2004; Einum 2005; Imre et al. 2005). In freshwater fishes, density-dependent growth (e.g., Lorenzen & Enberg 2002), mortality (e.g., Elliot 1994), reproduction (e.g., Wootton 1990) and movement (e.g., Rose et al. 2001) is well documented. The detailed knowledge of the biology and ecology of salmonids and a wealth of theoretical and empirical evidence (e.g., Elliott 1993; Elliott 1994; Cattaneo et al. 2002) suggest the crucial importance of endogenous mechanism regulating population dynamics of salmonids – especially in stable systems where abiotic influences are rare – but the quantification of the relative importance of density-dependent and -independent factors is still uncertain. Given the territorial behaviour of stream-living salmonids and food requirement, there is clearly a limit

on the number of fish that any stream can support, with carrying capacity depending on species, age of fish, nature of the habitat, food availability and time of the year (Milner et al. 2003). In his influential review, Sinclair (1989) found that in species with high reproductive rates, like fish and insects, density-dependence occurred mostly early in life. In a long-term study on sea trout, Elliott (1993) showed density-dependent mortality in the early stages of life (30–70 days after hatching) after which mortality was influenced only by density-independent factors. The density-dependent mortality in the early stages of life is believed to be the result of strong competition for territory by newly emerged fish (Chapman 1966; Allen 1969; Elliot 1990; Grant & Kramer 1990). In a study on *Salmo trutta* L. populations living in 30 French stream reaches, Cattaneo et al. (2002) found a strong negative correlation between the discharge rate during the emergence period and density of *S. trutta* aged 0+, probably caused by the loss of 0+ fish due to the inability to maintain their stream position when water discharge is high: at high population density only

yearlings that find a shelter survive, while the others are flushed away by floods. Their study thus suggests that there can be an interaction between exogenous and endogenous or density-dependent factors in determining the survival of brown trout during the first year of life. Recently, Lobón-Cerviá & Rincón (2004) provided evidence of the importance of stream discharge on recruitment in a population of *S. trutta* living in Rio Chabatchos (Spain); the results obtained by Cattaneo et al. (2002) and Lobón-Cerviá & Rincón (2004) appear to confirm the context-dependent importance of density-dependent and -independent factors, the latter predominating in harsh environments. The assessment of the relative importance of endogenous and exogenous factors in the regulation of population dynamics and fish recruitment is particularly difficult for stream-living salmonids in non-experimental settings. Moreover, in species exhibiting high plasticity in body growth like salmonids not just survival but also body growth and size at sexual maturity can be affected by density-dependent mechanisms; population density can thus also influence the reproductive output (i.e., number of eggs produced), as fecundity is usually correlated with body size in salmonids. As argued by Jenkins et al. (1999) observational data and time-series analyses are often insufficient to detect endogenous mechanism regulating population dynamics and should be complemented by experiments in which environmental variation is minimised or controlled for and density ranges from very low to very high values.

The aim of the present work is to test the hypothesis of density-dependent survival in the first year of life for translocated marble trout *Salmo marmoratus* (Cuvier 1817) populations in two pristine Slovenian streams, combining observational data and simulation analysis. Marble trout is a species of particular conservation interest, being endemic only in a restricted geographical area belonging to the Adriatic Basin, in particular in the basin of Po river in Northern Italy (Sommani 1961; Forneris et al. 1990), in the Adriatic Basin of former Yugoslavia (Povz 1995) and Albania (Schoffmann 1994). Since the beginning of the last century (the first documented case dates back to 1906, Povz et al. 1996), *S. trutta* of different origins have been introduced into the geographical area where marble trout occurs. The introduction of *S. trutta* quickly led to the creation of hybrid populations (Berrebi et al. 2000) which displaced the native ones. At present, only eight pure marble trout populations were discovered in isolated streams in the upper reaches of the Soca and Idrijca river basins in Slovenia (Berrebi et al. 2000; Snoj et al. 2000). Here we report on a 9-year on-going study of translocated pure marble trout populations in two Slovenian streams, designed with the purpose of exploring the population dynamics

of the endangered species marble trout (for a full report on the Marble Trout Rehabilitation Project refer to Crivelli et al. 2000). The investigation of density-dependent survival of newly emerged trout is performed by combining a classical life table analysis (Dempster 1983; Stiling 1988; Sinclair 1989; Auerbach et al. 1995) with simulations following a Monte Carlo approach.

Material and methods

Study area and species description

The Marble Trout Rehabilitation Project started in 1993 in the upper part of the Idrijca River basins belonging to the Adriatic Basin of Slovenia (Fig. 1). The Idrijca River basin presents a well-preserved environment, that is, remarkable quantity and quality of water, reduced agricultural and industrial activities, absence of erosion due to numerous deciduous forests – mainly *Fagus sylvatica* – low human population density and numerous areas officially protected, such as the Triglav National Park. Fly fishing is one of the main attractions for tourists and one of the most profitable economic activities in the region, attracting many anglers from abroad.

Marble trout is the only fish species present within both the experimental streams (Gorska and Zakojska), both located in headwaters and with no predation or fishing activities. Streams length and topographical features were acquired from surveyor field investigations and from available GIS (source: Surveying and Mapping Authority of the Republic of Slovenia). Habitat features of Zakojska and Gorska are presented in Table 1. The streams can be divided in sectors (11 in Gorska, seven in Zakojska) separated by impassable waterfalls, so trout can only move from upstream sectors to downstream sectors. The stream bed of Gorska consists mainly of bedrock slides and is narrower than that of Zakojska and its flood plain is almost absent, with few shelter areas. On the contrary, in Zakojska, in case of flood the stream can overflow its bank on a wide area with riparian forest creating new suitable habitat for marble trout. Rainfall data has been acquired since 1961 (ARSO, Environmental Agency of Slovenia). The annual mean precipitation is 2400 mm with October and November being the most rainy months. Annual rainfall in the study period ranged from 1764.5 mm in 2003 to 2495.7 mm of 2000. Monthly rainfall in March was extremely variable ranging from 0.9 mm during the severe drought of 2003 to 479.5 mm of 2001. In April a threefold variation was observed during the study period, ranging from 119.7 mm in the 2002 to 362.8 mm in 1999.

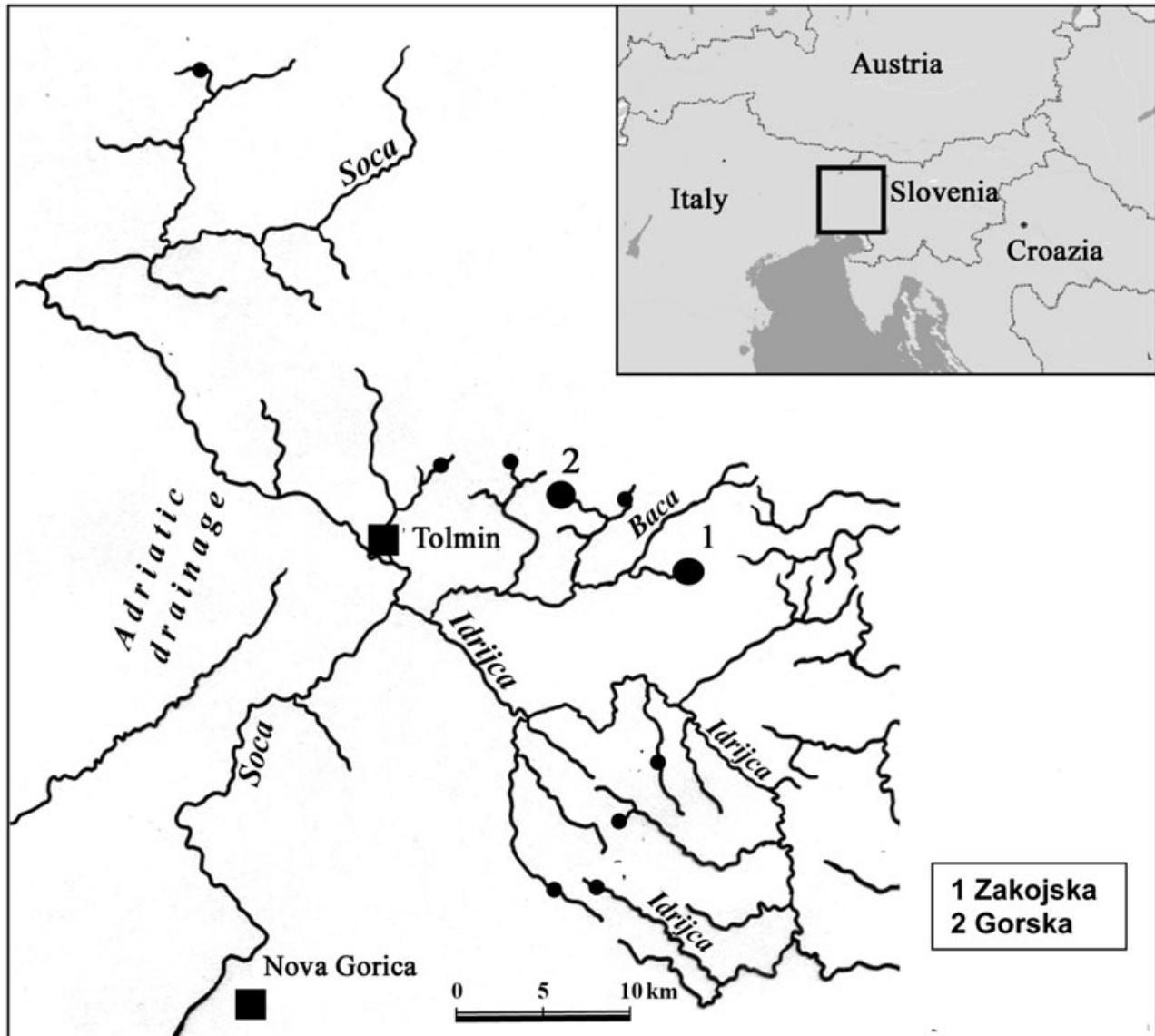


Fig. 1. Map showing the location of *Salmo marmoratus* populations introduced in Gorska and Zakojska. The Soca and Idrija river basins lie in the northwestern part of Slovenia and belong to the Adriatic Basin.

Table 1. Main habitat features of Zakojska and Gorska, from spring to downstream close to the lowest part of the experimental stream with pure marble trout.

Main features	Zakojska	Gorska
Watershed characteristics		
Watershed area (m ²)	62,600	21,900
Stream length (m)	2480	1940
Land average slope (%)	60.65	64.35
Surface stream average slope (%)	22.5	22.8
Experimental stream characteristics		
Length (m)	1238	845
Surface area (m ²)	3544	1805
Pool surface (m ²) (% of total surface)	895 (25.3)	685 (38)
Altitude range (m.a.s.l.)	578–728	400–514
Number of sectors	7	11
Benthos biomass (mg m ⁻²)	14,638	11,446

Water temperature of the streams was recorded with recording temperature loggers (Optic Stoneway model; Onset Corporation, Bourne, MA, USA) at hourly intervals. Annual average water temperature during the study period in Gorska and in Zakojska varies between 8.2–9.0 and 7.6–8.2 °C, respectively.

Marble trout present a high plasticity in growth rates; individuals of marble trout with weight up to 25 kg have been found in the lower reaches of the Soca River (Fumagalli et al. 2002) while in the study area the maximum recorded weight was 520 g. In the study area, maximum recorded age for marble trout was 6 years. Marble trout feed generally on bottom-dwelling organism and cannibalism by adult marble trout was observed. Spawning takes place in

November to December while marble trout eggs hatch generally in March, with emergence occurring in April to May. Data and direct observation in streams of Soca and Idrijca river basins where pure marble trout occurs show evidence of a certain amount of repetition in reproduction (iteroparity).

Sampling procedure and data collection

In 1994, wild genitors from one of the remnant pure populations (Zadlascica) were taken in November, stripped in the hatchery and put back to their stream. Fish produced were reared for 1 year and then stocked in 1996 in two fishless streams of the Baca River basin – Zakojska and Gorska – isolated from the hybridisation zone by natural impassable waterfalls. Each released individual was marked with Carlin tags that do not affect survival and growth of marked fish (Kolari et al. 1998). Since 1996, an annual monitoring program has been carried out in order to assess the long-term persistence and the population dynamics of those translocated pure populations. Sampling was performed every June from 1996 to 2004 on the whole length of each stream starting from downstream to the upstream extent, consequently the whole population is sampled every year. A gasoline-powered, portable backpack electrofishing unit was used. Every stream was electrofished two times to produce a multiple-pass removal estimate of trout abundance using Microfish 3.0 (Van Deventer & Platts 1989). Age designation follows standard terminology; marble trout in the first year of life were denoted as 0+ and in the second year, subsequent to winter annulus formation, as 1+. All captured fish aged $\geq 1+$ were anaesthetised with benzocaine, marked with Carlin tags made in Sweden (Institute of Freshwater Research), measured for total length (L_T , to the nearest mm) and weight (W , g) and if sampled for the first time the adipose fin was removed. Then marble trout were returned alive near the point of capture. Age was determined by tag examination. At first marking, scales were taken to assess the age of the fish. The small size of marble trout aged 0+ prevents their sampling in June and therefore they are not taken into account in this study. No sexing of trout caught could take place at that time of the year. Marble trout hatched in the streams aged 1+ were sampled each year from 2000 to 2004 included.

As no data on stream flow were available, rainfall was used as surrogate of stream discharge. Monthly rainfall were recorded at Rut precipitation station, the nearest one available to both streams, for the whole period of the study (1996–2004). In order to estimate fecundity, 33 wild females – aged from 3 to 5 years old – from the Zadlascica pure population were stripped in the fish farm (Tolminka, Tolmin, Slovenia). Females were put back to their stream after stripping. An

assessment of successful spawning of pure marble trout living in the study area using paternity investigation showed as minimum and maximum age for spawning for marble trout females 3 and 5 years old, respectively. First spawning occurs at a minimum length of 200 mm. All females aged 3+ and 4+ and exceeding 200 mm spawn successfully. Approximately 20% of marble trout females aged 5+ spawn successfully, with spawning probability being independent of body length.

Length–fecundity relationship

We estimated a linear relationship between body length L and number of eggs $F(L)$ produced by a female, such as:

$$F(L) = \alpha + \beta L + \varepsilon(0, \sigma_\varepsilon) \quad (1)$$

where ε is a normal error with mean equal to zero and variance σ_ε estimated through least square regression on available data along with the slope β and the intercept α .

Marble trout density

Density of marble trout at the stream level was computed by dividing the total or age-specific number of marble trout estimated from multiple-pass removal by the overall pool surface of the stream, as it offered the best quantification of instream areas suitable for marble trout. Difference in mean marble trout density between streams during the study period was tested by Kruskal–Wallis test.

Survival σ_0

Survival σ_0 from eggs to age 1+ was estimated by using the age–cohort data sampled in the two streams between 1998 and 2004 as described hereafter. Let $\bar{N}_x(t)$ be the estimated number of marble trout (males + females) aged x in the reproductive phase ($3+ \leq x \leq 5+$) at year t , $\bar{N}_{1+}(t+2)$ is the estimated number of marble trout aged 1+ at year $t+2$, that is, the progeny of marble trout which successfully spawned 2 years before. According to field observations and experiments performed in the fish farm, marble trout aged less than 3 years old or smaller than 200 mm are assumed not to be reproductive yet. The fraction of x years old females ($3+ \leq x \leq 5+$) that actually spawn is indicated with β_x , sex ratio is assumed to be 1:1. Thus, for each year for which data are available ($t = 1998, 1999, \dots, 2002$), the expected number $\hat{S}_x(t)$ of x years old females actually spawning was computed as $0.5\beta_x\bar{N}_x(t)$. As sampling campaigns take place in June, eggs laid in the late autumn of year t by $\hat{S}_x(t) = 0.5\beta_x\bar{N}_x(t)$ reproductive females hatched in early spring of year $t+1$ and $\bar{N}_{1+}(t+2)$ yearlings

were then sampled as 1+ in June of year $t + 2$. σ_0 was thus computed as the ratio between $\bar{N}_{1+}(t + 2)$ and the estimated total number of eggs $\hat{E}(t)$ laid in year t .

In order to estimate the number of eggs laid by each reproductive female, information on the actual female length is required. As sampled marble trout were not sexed, we used the observed age-specific discrete distribution $\bar{\Lambda}(l/x, t)$ of length l of marble trout sampled in year t to derive information on female length by means of a Monte Carlo approach, as described here after:

- 1 a set of length values $L_i(x, t)$ [$i = 1, 2, \dots, \hat{S}_x(t)$] was drawn randomly from the observed age-specific discrete distribution $\bar{\Lambda}(l/x, t)$;
- 2 expected fecundity $F(L_i(x, t))$ of each spawning female of length $L_i(x, t)$ in year t was then estimated by using Eqn (1);
- 3 the total number of eggs $\hat{E}(t)$ produced in year t was computed as the sum of the eggs produced by each spawning female, that is $\hat{E}(t) = \sum_{i=1}^{\hat{S}_x(t)} F(L_i(x, t))$;
- 4 survival $\hat{\sigma}_0(t)$ was then computed as the ratio between the estimated number $\bar{N}_{1+}(t + 2)$ of trout aged 1+ in years $t + 2$ and the estimated total number of eggs $\hat{E}(t)$ produced by their parental stock.

For each stream, the procedure (1–4) was repeated 10,000 times for each of the five pairs of years for which $\bar{N}_x(t)$ and $\bar{N}_{1+}(t + 2)$ data were available and the mean value of survival $\sigma_0(t)$ and number of eggs produced $\hat{E}(t)$ were then computed from each of the five distributions of 10,000 replicates. Density of eggs produced $\hat{E}_D(t)$ was computed by dividing $\hat{E}(t)$ by the overall pool surface of the stream.

Density-dependence effect

Density-dependence hypotheses were tested by exploring the relationship between survival σ_0 and: (i) density $\hat{E}_D(t)$ of eggs produced (eggs m^{-2}); (ii) total density of marble trout in June of year $t + 1$ (trout m^{-2}); and (iii) the density of marble trout aged 1+ in June of year $t + 1$. The dependence of survival σ_0 on trout density at year $t + 1$, when eggs hatch, was tested as the main density-dependent regulating processes in salmonids act mostly during the juvenile phase (Elliott 1993; Milner et al. 2003). Significant departures of residuals from normality were assessed by chi-square goodness-of-fit test.

Effect of exogenous factors

To test the importance of environmental factors, we used monthly rainfall in February, March, April, May and suitable combinations of monthly rainfalls at year

$t + 1$ (bimonthly and trimonthly rainfalls) – just prior to and during marble trout hatching (March) and emergence (April to May) – as a proxy indicator of the unknown stream flow. We thus tested whether rainfall was able to explain the residuals of the $\sigma_0 - \hat{E}_D(t)$ relationship.

Results

The relationship (1) between length of females and number of eggs produced was significant ($P \ll 0.01$, $R^2_{adj} = 0.5$, $\alpha = -749.97 \pm 94.24$, $\beta = 3.8 \pm 0.69$).

Basic statistics relative to length and weight of marble trout in the reproductive phase sampled in Zakojska and in Gorska are reported in Table 2 while Fig. 2 shows the estimated density of marble trout (ind m^{-2}) in both streams from 1998 to 2004, that is, without considering the first two years in which densities were obviously determined only by the translocation. Mean density of marble trout across years is significantly different between the two streams (Kruskal–Wallis test, $P < 0.05$).

Table 3 reports the input parameters $\bar{N}_x(t)$ and $\bar{N}_{1+}(t + 2)$ for the Monte Carlo simulation. Survival from eggs to 1+ (σ_0) estimated following the Monte

Table 2. Number and length of marble trout in the reproductive phase sampled in Zakojska and in Gorska from 1998 to 2002.

Stream	Zakojska		Gorska	
	<i>N</i>	Length \pm SD (mm)	<i>N</i>	Length \pm SD (mm)
3+	278	216.14 \pm 35.78	136	227.11 \pm 45.81
4+	100	249.92 \pm 36.80	52	267.56 \pm 42.61
5+	56	268.16 \pm 40.05	11	315.00 \pm 32.34

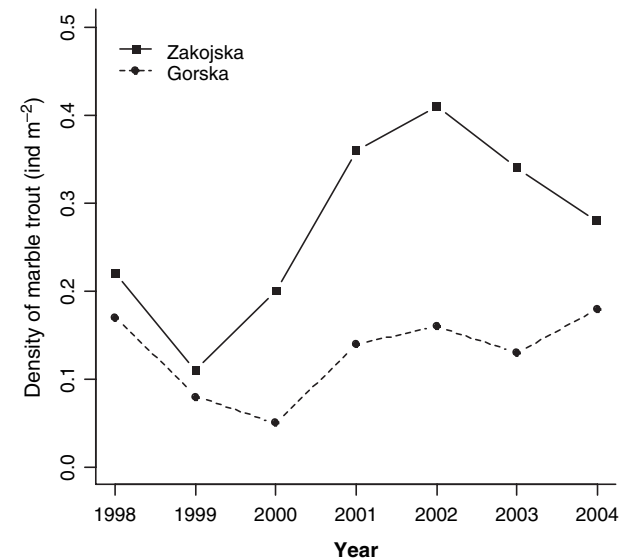


Fig. 2. Estimated total density of marble trout (ind m^{-2}) in Zakojska and in Gorska from year 1998 to year 2004.

Table 3. Estimated number of marble trout in the reproductive phase (age 3+ to 5+) and recruits (1+) in Zakojska and in Gorska between 1998 and 2004.

Year	Zakojska				Gorska			
	Age 1+	Age 3+	Age 4+	Age 5+	Age 1+	Age 3+	Age 4+	Age 5+
1998	–	196	0	0	–	118	0	0
1999	–	0	95	0	–	0	51	0
2000	122	0	0	56	23	0	0	11
2001	166	7	0	0	72	1	0	0
2002	122	75	5	0	33	17	1	0
2003	55	–	–	–	7	–	–	–
2004	77	–	–	–	65	–	–	–

Marble trout aged 1+ born in the river in year $t + 2$ are the progeny of the reproductive parental stock in year t .

Carlo approach ranges from 0.015 to 0.13 in Zakojska and from 0.003 to 0.08 in Gorska (Fig. 3).

A strong negative correlation was found in both streams between density of eggs produced and survival from eggs to 1+, well explained by the negative power curve $\sigma_0 = a\hat{E}_D^{-\gamma}$ (Fig. 3: Zakojska, $P < 0.01$; Gorska, $P < 0.05$). The two estimated curves were compared by performing a F -test (Motulsky & Christopoulos 2003) and resulted not significantly different from each other ($P > 0.05$). No significant correlations were found between σ_0 and total density of trout at year $t + 1$ and σ_0 and density of trout aged 1+ at year $t + 1$ either by testing the relationship through linear models and power curves.

In Zakojska, March rainfall explained a significant proportion of the variance in σ_0 not already explained by the density of eggs produced ($P < 0.05$, $R^2 = 0.76$) (Fig. 4), while the correlation between rainfall and σ_0 residuals was not significant in Gorska.

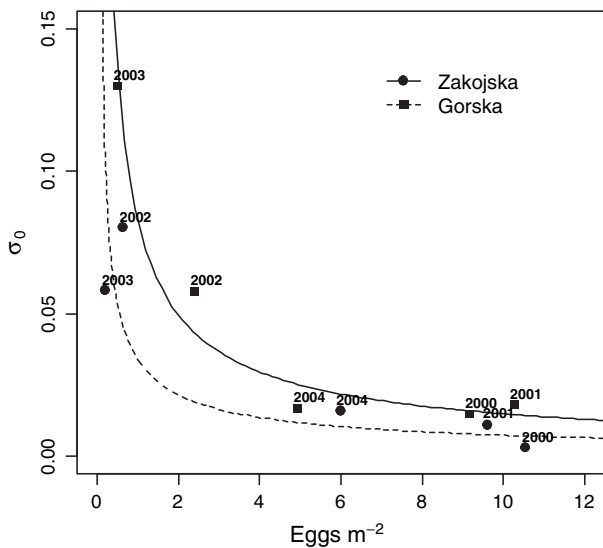


Fig. 3. Relationship between survival from eggs to 1+ σ_0 and the density of eggs produced \hat{E}_D for Zakojska and Gorska in the form $\log \sigma_0 = a + \gamma \log \hat{E}_D$ (Zakojska: $a = -2.48 \pm 0.22$, $\gamma = -0.75 \pm 0.13$, $P < 0.01$, $R^2 = 0.9$; Gorska: $a = -3.38 \pm 0.38$, $\gamma = -0.66 \pm 0.11$, $P < 0.05$, $R^2 = 0.7$).

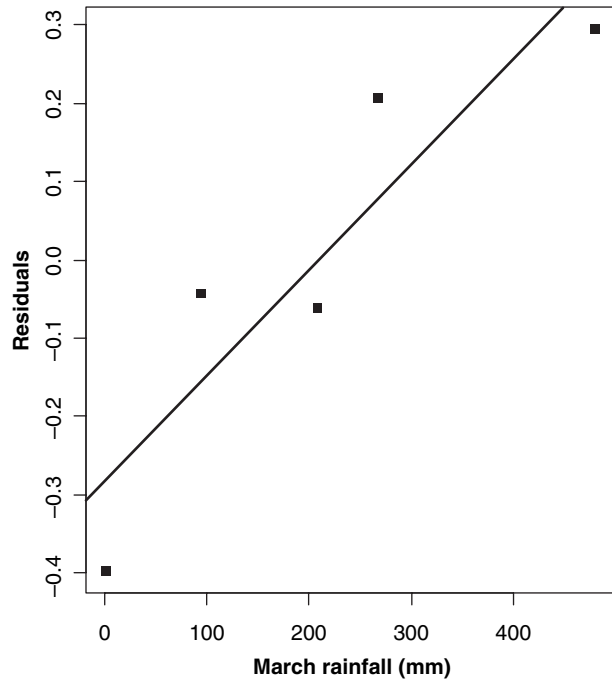


Fig. 4. Relationship between rainfall in March at year $t-1$ and the residuals from the density of eggs- σ_0 model ($P < 0.05$, R^2 adj = 0.76).

February, April and May rainfalls and bimonthly and trimonthly combinations of rainfalls did not explain a significant proportion of the variance in either streams.

Discussion

Our analysis confirms the importance of both exogenous and endogenous factors in regulating the number of marble trout aged 1+ in two Slovenian streams. Density of eggs was the major determinant of survival σ_0 in both streams in the period 2000–2004 in both streams, while rainfall prior to juveniles emergence appears to play an important role in Zakojska. Yearling survival remarkably increased when eggs density was low. For similar density levels, survival from eggs to age 1+ is systematically lower in Gorska than in Zakojska. Although the difference is not significant – also because of the low number of data used to fit the density-dependent relationship – the fact that for similar egg densities σ_0 is larger in Zakojska than in Gorska was somehow expected: in fact, Gorska is characterised by a less suitable habitat (more fragmented, shorter sectors, less shelter, narrower stream section) than Zakojska for survival of marble trout, which is also evidenced by the lower marble trout density observed in Gorska than in Zakojska during the study period. As noted in a recent paper by Einum (2005), exogenous forces may actually interact with density-dependent processes. Lobón-Cerviá & Rincón (2004) found a strong correlation between recruitment

and the availability of suitable microhabitat for juveniles shortly after emergence in Rio Chabatchos (Spain) and a limited role of density-dependent mechanism in regulating recruitment. On the contrary, using the same brown trout data provided by Lobón-Cervía & Rincón (2004), Einum (2005) suggested a different approach to assess the contribution of density-dependent factors on population regulation. By considering the relationship between loss rates over the period from egg to 4-month-old juveniles and an index of initial juvenile density, Einum (2005) found strong support for density dependence in three of the four sites examined by Lobón-Cervía & Rincón (2004). Einum (2005) suggested that it is the presence and not the absence of endogenous regulation that causes the population size to track environmentally induced variation in the limiting factor (juvenile habitat). In our analysis, March rainfall at year $t + 1$, when hatching occurs, explained a significant part of the variance in σ_0 not already explained by the density of eggs produced in Zakojska. As rainfall is a proxy-indicator of stream flow, our result is opposite to that obtained by Cattaneo et al. (2002), who found a negative correlation between water discharge and yearling survival. Our hypothesis is that the relationship we found can be explained by the fact that in Zakojska the scarce availability of suitable habitats is a limiting factor for yearling settlement and survival. As a consequence, the positive relationship between rainfall and σ_0 could be related to the increasing availability of suitable microhabitat for juveniles with increasing rainfall, at least in the range of rainfalls observed in the study period. This does not happen in Gorska, where, given the morphological features of the stream, higher water flows do not provide an increasing availability of suitable microhabitat for juveniles. On the other hand, we believe extreme river flows may determine a reduction of σ_0 , by flushing away or killing young marble trout. This is what actually happened in mid-October 2004 in Gorska when a debris flood – probably with a time of return of 50 years – wiped out the entire population of juveniles and adults as observed during our sampling campaign in June 2005, when no trout was found in Gorska. In Zakojska, subject to the same rain pattern of Gorska, the population maintained almost the same size as before the flood. This shows that stream and watershed features and the resulting hydrological regime may be important determinant of the observed pattern of population dynamics. Anyway, as the results are based on a limited time series of data, our preliminary conclusions on the role of stream flow (of which rainfall is a surrogate) on survival during the first year of life of marble trout need to be confirmed by further analysis on a longer time series of data. As noted by Rose et al. (2001) a promising trend is the recent focus

on how the interaction between environmental stochastic fluctuations and density-dependent processes regulates the long-term dynamics of fish populations. Our results highlight the importance of density-dependent and environmental factors in determining the survival of marble trout during the first year of life; as recruitment is one of the major determinants of population size in salmonids (e.g., Lobón-Cervía & Rincón 2004), we believe our findings could significantly enhance the comprehension of marble trout population dynamics and the effectiveness of rehabilitation projects.

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