

Individual growth and its implications for the recruitment dynamics of stream-dwelling marble trout (*Salmo marmoratus*)

Vincenzi S, Crivelli AJ, Jesensek D, De Leo GA. Individual growth and its implications for the recruitment dynamics of stream-dwelling marble trout (*Salmo marmoratus*).

Ecology of Freshwater Fish 2010: 19: 477–486. © 2010 John Wiley & Sons A/S

Abstract – The role of density-dependent individual growth in the recruitment dynamics of fish populations has rarely been analysed in a quantitative framework. Variations of mean size of juveniles in response to changes in population densities have frequently been observed in salmonids and it has been shown that body-size differences at the juvenile stage can persist through the sub-adult and adult stage. As fecundity and sexual maturation are often a function of body size, inter-cohort variations in individual growth may ultimately affect the reproductive output and, consequently, the amount of yearly recruitment. Here, we present a simulation analysis investigating the effects of density-dependent growth on the reproductive output and, ultimately, on the population dynamics of stream-dwelling salmonids. The demographic model used for the numerical analysis was parameterised using marble trout *Salmo marmoratus* as a reference species and explicitly accounted for the occurrence of major floods events causing the population to collapse to very low densities. Our simulations showed that density-dependent individual growth is a powerful mechanism to foster population resilience through compensatory recruitment. In addition, we argue that density-dependent growth also helps regulate recruitment at high population densities. We show that even slight variations in the growth trajectories of fish substantially affect the size and the dynamics of the population.

**S. Vincenzi¹, A. J. Crivelli²,
D. Jesensek³, G. A. De Leo¹**

¹Dipartimento di Scienze Ambientali, Università Degli Studi di Parma, Parma, Italy, ²Station Biologique de la Tour du Valat, Le Sambuc, Arles, France, ³Tolmin Angling Association, Most na Soci, Slovenia

Key words: marble trout; density-dependent individual growth; recruitment dynamics

S. 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 June 7, 2010

Introduction

The issue of which factors control the abundance of natural populations is central to biology and has spurred a ongoing debate on the relevant mechanisms that prevent populations from growing without bound. Both environmental factors (usually operating in a density-independent way) and density-dependent processes affect the abundance of a persistent population. However, it is generally accepted that only intrinsic mechanisms can provide the necessary density-dependent feedbacks that make a population decrease when it is too abundant, and increase when it is too sparse (e.g., Turchin 1995). Density-dependent effects on population dynamics have frequently been observed in

salmonids (e.g., Rose et al. 2001; Milner et al. 2003) and it is widely believed that density-dependent mortality during the juvenile phase is the most important endogenous mechanism of population regulation in salmonids (e.g., Elliott 1994; Milner et al. 2003). On the other hand, failure to detect consistent stock-recruitment relationships in stream-living salmonids led Lobón-Cerviá & Rincon (2004) to suggest that exogenous factors and their interplay with habitat features, in particular juvenile habitat, are the dominant drivers of population dynamics with little or no operation of density-dependent processes. The existence of multiple regulatory mechanisms in fish populations is well accepted, but the role for population regulation of processes other than

density-dependent survival at the larval/juvenile stage still remains very controversial (Lorenzen 2008). In addition, most theoretical work has focused on density-dependent mechanisms that prevent a population from growing unbounded while mechanisms enhancing population resilience, i.e., a prompt recovery after a major population crash, have attracted less attention.

Density-dependent individual growth has been detected in the juvenile stage in a number of salmonid species (e.g., brown trout *Salmo trutta* L., Jenkins et al. 1999; Lobón-Cerviá 2007; Atlantic salmon *Salmo salar* L., Imre et al. 2005; for a meta-analysis of density-dependent growth in juvenile salmonids refer to Grant & Imre 2005). The emerging relationship between average growth rates and density of 0+ individuals is generally well described by a negative power function (e.g., Grant & Imre 2005). As for postjuvenile phases, Utz & Hartman (2009) found that adult growth and excess energy acquisition was density-dependent in brook trout *Salvelinus fontinalis*, but only during periods when temperatures were warm and energy intake was low. Many ecologists suggested that exploitation competition for drifting prey rather than space limitation may be responsible for density-dependent individual growth (e.g., Jenkins et al. 1999; Imre et al. 2005). Conversely, Ward et al. (2007) found that competition for space also yields concave density–growth curves. Whether the observed pattern is due to exploitative or interference competition or a combination of the two is still a matter of debate (Ward et al. 2007).

Density-dependent individual growth may contribute to population regulation at the adult stage. In fact, a tight relationship is commonly observed between body size and sexual maturation rates, egg production and spawning frequency (e.g., Rose et al. 2001). As a consequence, larger female fish are expected to produce more eggs. Moreover, if minimum body size at sexual maturity is insensitive to variation in density, time to reach sexual maturity can substantially change in response to variation of population densities affecting body size growth (Rochet 1998; Beverton 2002). Beverton & Holt (1957) acknowledged the existence of density-dependent growth in recruited fish but claimed that its importance for population regulation was small with respect to the other compensatory responses, such as density-dependent survival. However, this could be caused by an asymptotic stock–recruitment relationship where variations in body size had little effect on population dynamics. Hence, the implications of density-dependent individual growth in population regulation and resilience remains little appreciated and its potential is still controversial (e.g., Rose et al. 2001).

Natural selection for increasing lifetime reproductive success shapes the life-histories of a given

population in a given place, where life-histories reflect the expression of traits closely related to fitness, such as age and size at maturity, reproductive output and the timing of the expression of these traits through the lifetime (Hutchings 2003; Kozłowski 2006). We could thus expect that density-dependent growth might provide an adaptive advantage in a stochastic environment with respect to a variant species that do not exhibit such a trait, i.e., whose individual growth pattern is invariant with respect to changes in population density caused by exogenous events. However, the contribution of density-dependent individual growth in recruitment regulation has been little investigated in a quantitative framework in salmonids, and both observational and experimental studies have mostly focused on the detection of density-dependent individual growth at young-of-the-year stage. In contrast, the degree to which size differences in juveniles (both intra- and inter-cohort) caused by fluctuations in population density persist through the adult stage (the carry-over effect), and density-dependent effects on individual growth during the post-recruit phase have been scarcely investigated in freshwater fishes. Both empirical evidence as well experimental result for a variety of species (fish, lizards, snakes, humans, birds, etc.) show that the environmental conditions experienced early in life may affect growth of individuals through the lifetime as well as several related properties, such as metabolism and immunocompetence (see Lindstrom 1999 for a review of carry-over effects). Therefore, presently observed phenotypic traits may have developed through ontogenic trajectories originated in early life phases (Schlichting & Pigliucci 1998).

In a previous work, Vincenzi et al. (2008a) showed that density-dependent individual growth fosters population resilience in stream-dwelling salmonids after a population collapse caused by severe flood events. In this work, we used marble trout (*Salmo marmoratus*) as a model system to test whether density-dependent growth can provide recruitment regulation. We explored multiple scenarios through a simulation analysis based on a demographic model of marble trout dynamics accounting for the occurrence of flood events. We specifically investigated recruitment regulation at either high and low population densities. We also explored whether slight changes in body growth trajectories of fish could substantially alter risk of extinction and population abundance of marble trout.

Materials and methods

We developed a data-driven individual-based model (IBM) of population dynamics of marble trout living in Slovenian streams. Full details are reported in Vincenzi et al. (2008a) and briefly described below.

Data collection

Data for the estimation of demographic traits of marble trout were obtained from the tag-recapture monitoring of two marble trout populations living in Slovenian streams (Zakojska and Gorska) from 1996 to 2004 (Gorska) and from 1996 to 2008 (Zakojska). In this article, we report only demographic traits and compensatory responses of the population of Zakojska. The length of Zakojska is 1238 m with a pool surface of 895 m². The annual mean precipitation from 1961 to 2007 was about 2412 ± 307 mm (mean ± SD) with October and November, the rainiest months.

Sampling was performed every June since 1996 on the whole length of each stream. Age-0 individuals were not marked as their small size in June prevented their sampling. To avoid possible negative effects of Carlin tagging on small fish, only marble trout aged ≥1 and longer than 115 mm were tagged. Age was determined by tag examination or, in case of first sampling or tag loss, by reading scales. Autumnal floods are a major threat to the persistence of marble trout populations living in Slovenian streams, causing sudden drops in population size (Vincenzi et al. 2008a). Although the occurrence of floods during fall is common, the severity and frequency of floods vary greatly from year-to-year depending on the duration, frequency and intensity of rainfall. Local geomorphology may also play a role in the flood dynamics; brief and violent floods, which can flush trout away, typically occur in high gradient constrained channels. Mean ± SD number of marble trout ≥ age-1 in Zakojska was 270 ± 82 between 1997 and 2007, a period during which major flood events did not occur. However, the population dramatically collapsed after a severe flood in

November 2007 from 264 individuals in June 2007 to 11 and 15 individuals in 2008 and 2009, respectively.

Demographic parameters

Maximum likelihood estimates of survival and capture probabilities for sub-adults and adults were estimated by using the program MARK (White & Burnham 1999). Survival probabilities (σ_A) for sub-adults (immature fish, aged ≤2+) and adults (mature fish, aged ≥3+) were both density- and size-independent (Vincenzi et al. 2008b). Moreover, as they were estimated without considering the years following the flood event in Zakojska of 2007, survival probabilities (σ_A) are estimates in absence of major flood events. Results are reported in Table 1.

Vincenzi et al. (2007a) found a significant effect of density of eggs (E_D) on survival from egg to age 1 (σ_0) in marble trout living in Slovenian streams, well described by a negative power law curve in the form:

$$\sigma_0 = aE_D^{-\gamma} \quad (1)$$

Individual growth was modelled in two alternative ways. First, we assumed that mean growth in body length can be described through a density-independent Von Bertalanffy model in the form:

$$\bar{L}_x = L_\infty \left(1 - e^{-k(x-x_0)} \right) \quad (2)$$

where x is age (years, y) and, maximum length L_∞ (mm), Brody's growth coefficient k (y^{-1}) and the age at which length equals zero x_0 (y) were computed based on available data (Vincenzi et al. 2007b).

Additionally, evidence of density-dependent individual growth was found for the marble trout popu-

Table 1. Parameters of the individual-based model of population dynamics for the population of Zakojska. In the simulations, model parameters were randomly drawn at each time step of 1 year from the uniform distribution over their respective 95% confidence interval.

Sub-model	Parameter	Exp. value	95% CI	Description
Density-dependent first-year survival model	σ_A	0.57	0.53–0.62	Adult survival
	a	0.084	0.074–0.093	Constant of the power curve model of first-year survival
	γ	-0.75	-0.85 to 0.65	Scaling exponent of the power curve model of first-year survival
Linear model of egg production	α	-749.97	-944.68 to -525.26	Intercept of the linear model of egg production
	β	3.8	2.45–5.15	Slope of the linear model of egg production
Von Bertalanffy body growth model	L_∞	318.24	294.69–351.27	Asymptotic length
	k	0.34	0.27–0.41	Brody's coefficient
	x_0	-0.34	-0.49 to -0.20	Age at which length is equal to 0
Density-dependent body growth model	c_1	98.49	92.11–107.13	Age-specific constants of the power curve model of density-dependent growth
	c_2	146.94	137.49–161.01	
	c_3	179.47	170.73–195.93	
	c_4	206.44	192.64–224.64	
	c_5	230.44	201.35–265.04	
	δ_1	-0.11	-0.16 to -0.06	Age-specific scaling exponents of the power curve model of density-dependent growth
	δ_2	-0.12	-0.17 to -0.07	
	δ_3	-0.12	-0.16 to -0.07	
	δ_4	-0.12	-0.16 to -0.07	
	δ_5	0.10	-0.18 to -0.01	

lations (Vincenzi et al. 2007b, 2008a). The mean length of the individuals of a cohort at age $1 \dots 5 (\bar{L}_1 \dots \bar{L}_5)$ was negatively correlated with total density of marble trout aged ≥ 1 across the whole stream when the cohort was in its first year of life (D_U , overall population density experienced as underyearlings), clear evidence of a carry-over effect of early density (and early growth) on mean growth of the cohort through the lifetime. Therefore, the relationship between population density and expected mean individual length of fish in a cohort was described by an age-specific negative power curves in the form:

$$\bar{L}_x = c_x D_U^{-\delta_x} \quad (3)$$

where the scaling factor δ_x and the constant c_x were estimated for each age class $x = 1, 2, \dots, 5$ on the available data. In contrast, our field data suggest that density at age x has no influence on body growth from age x to $x + 1$ when $x \geq 1$ (Vincenzi et al. 2008b).

As no field data were available on egg production, we relied on experiments performed in fish farm (Tolminka, Vincenzi et al. 2008c) on *S. marmoratus* to study the relationship between body size and number of eggs produced. Model selection using AIC showed that the number of eggs produced by marble trout E is related to total length L of female by the linear relationship:

$$E = \alpha + \beta L \quad (4)$$

Minimum and maximum age for spawning for marble trout females living in Slovenian streams was 3+ and 5+, respectively. All females aged 3 and 4 and exceeding 200 mm spawned successfully. Approximately 20% of marble trout females aged 5 spawned successfully, with spawning probability being independent of body length (Meldgaard et al. 2007). In the marble trout population of Zakojska, egg size is not related to body size (Simone Vincenzi, unpublished data).

The model of population dynamics

Demographic parameters reported in Table 1 were used to design an IBM of population dynamics with a time step of 1 year incorporating both environmental and demographic stochasticity. Values of parameters included in the model of population dynamics were randomly drawn at each time step from the uniform distribution over their respective 95% confidence interval (Table 1), except for parameters of the growth models.

The number of marble trout in each age class was computed as follows:

$$\begin{cases} N_{x+1,t+1} = \sigma_x(t) N_{x,t} & x = 1, 2, \dots, 5 \\ N_{1,t+1} = \sigma_0(t, E_{D,t}) E_{D,t} \end{cases} \quad (5)$$

Early survival σ_0 was estimated by using Eq. (1), while annual survival of marble trout aged ≥ 1 was randomly drawn at each time step from the uniform distribution over the 95% confidence interval. Bernoulli trials were run to define if marble trout survived or died.

The number of eggs produced by female trout (sex ratio was assumed to be 1:1) was computed by using Eq. (4). Females were assumed to reach sexual maturity at age 3 and 4 when their length L exceeded 200 mm; 20% of females were sexually mature at age 5, independent of body length (Meldgaard et al. 2007).

The effect of floods on population size was simulated through a simple nonlinear fuzzy function linking October rainfall to a flood-induced mortality factor F that specifies the reduction in population size (%) induced by a flood event, ranging between 0 for low discharges to 70% (F_{\max}) for major flood events (the fuzzy function is fully described in Vincenzi et al. 2008b). In fact, October floods clearly proved to be a major threat to the viability of marble trout population in the study area: since 1993, three of eleven populations living in the study area went extinct after the impact of severe flood events occurred in autumn months. Stream discharge during the emergence period (April–May) seem to have a moderate influence on juvenile survival (Vincenzi et al. 2007a). The effects of floods on population size was computed as follows: first, we drew at each time step a rainfall value from the log-normal distribution of October rainfalls recorded from 1961 to 2007 in the study area, then we used the fuzzy function to derive the corresponding mortality (Vincenzi et al. 2008b), which allowed us to compute the resulting population size.

Simulation scenarios

We used the model to explore the recruitment dynamics, population persistence and recovery under two alternative hypotheses, i.e.; mean density-independent growth trajectories (DI) and density-dependent individual growth (DD).

In DD scenario, we used Eq. (3) to derive the mean individual length \bar{L}_x of trout aged x and actual length of each individual was then randomly drawn from a log-normal distribution with mean $\log \bar{L}_x$ and standard deviation equal to the mean of the standard deviations of the lognormal distributions fitted on cohort-specific L_x data (Vincenzi et al. 2007a). In DI scenario, the growth of each individual trout was computed with Eq. (2) by assuming Von Bertalanffy growth, with growth parameters L_∞ , k and x_0 randomly drawn for each individual from the uniform distribution over their respective 95% confidence intervals (Table 1) and kept constant through marble trout lifetime. We note that in the absence of environmental stochasticity

(i.e., constant model parameters), the two alternative growth models (i.e., DD and DI growth) yield the same population abundance at quasi-stable equilibrium which is very similar to the mean abundance observed in Zakojska between 1997 and 2007, a period in which no major flood event occurred (Vincenzi et al. 2008a).

We then used the model to assess whether slight variations in the growth trajectories of fish may influence egg production and, ultimately, population size, despite the bottleneck provided by density-dependent early survival. Specifically, we ran a set of simulations to explore the demographic consequences of a $\pm 5\%$ change in mean length-at-age in the case of a density-independent Von Bertalanffy growth model (scenarios DI-5% and DI+5%, respectively).

The IBM was run for the population of Zakojska for 1000 replicates of 100 years each for each of the four scenarios, i.e., DD, DI, DI-5% and DI+5%. Initial population size was set to 500 age-1 individuals. For each replicate, a set of demographic indexes was computed to evaluate population performances, in particular: (i) extinction risk, that is the percentage of simulations in which population abundance dropped below the 30 individual minimum number of marble trout observed in a viable populations (Dusan Jesensek, personal communication) during simulation time; (ii) mean adult population abundance across the simulation time, considering only the replicates in which the population did not go extinct, (iii) the mean per-capita number of eggs produced by sexually mature females, and (iv) the correlation $\bar{r}_{DD}(\pm SD)$ and $\bar{r}_{DI}(\pm SD)$, as the mean of the correlation r between number of eggs produced and population abundance estimated separately for each replicate of scenario DD and DI, using only the replicates in which the population did not go extinct. For part (iii) we computed the per-capita mean number of eggs produced: (i) at high density, that is when population size was ≥ 200 individuals (density $\geq 0.22 \text{ ind}\cdot\text{m}^{-2}$, as pool surface is 895 m^2); (ii) 4 years after a collapse in population size (population size lower than 70 individuals, density $\leq 0.08 \text{ ind}\cdot\text{m}^{-2}$), that is when the cohort experiencing a critical low density during the first growth period spawned for the first time. Per-capita mean number of eggs was also computed for different thresholds of population size to assess robustness of our results.

Results

Figure 1 shows sample trajectories of population dynamics with alternative modelling assumptions, namely scenario DI (Fig. 1a), DD (Fig. 1b) and $DI \pm 5\%$ (Fig. 1c). With density-independent individual growth the number of eggs produced was propor-

tional to population size (Fig. 1a, $\bar{r}_{DI} = 0.56 \pm 0.13$, $P < 0.05$ for each replicate), while with density-dependent individual growth (Fig. 1b) the correlation between the number of eggs produced and population size was lower ($\bar{r}_{DD} = 0.38 \pm 0.10$, $P < 0.05$ for each replicate). As shown in Fig. 2a, density-dependent growth reduced the risk of population extinction (scenario DD), with respect to a scenario in which individual growth was density-independent and followed the mean body growth trajectories estimated in the study area for marble trout (scenario DI). Slight variations in the mean body growth trajectories were sufficient to substantially decrease or increase (scenario DI+5% and scenario DI-5%, respectively) the risk of extinction (Fig. 2a), but overall the lowest risk of extinction was given by the scenario with density-dependent growth. Mean population size was higher when growth was density-dependent (Fig. 2b). The highest mean per-capita egg production at high densities was provided by scenario DI+5%, while 4 years after the occurrence of a severe flood events, the mean per capita egg production was higher with scenario DD (Fig. 2c).

Discussion

The results of our simulation analyses show that variation in individual growth contributes to the recruitment dynamics of resident salmonid marble trout. In particular, density-dependent individual growth may allow a faster recovery after population collapses due to severe disturbance events (Fig. 2a) by triggering the following chain of direct and indirect impacts (Fig. 3): first, severe floods remarkably reduce population abundance by flushing away or killing fish. Then, the individual growth rate of emerging cohorts increases due to a decreased density-dependent pressure. Females mature faster and produce more eggs, as both sexual maturity and per-capita egg production are size-dependent (Fig. 2c). The increased fertility and the relaxation of density-dependent first-year survival allow the surviving population to recover faster, thus reducing the risk of extinction. In Zakojska an increase in body length of marble trout aged 1 was observed after the flood event of November 2007 (112.68 ± 13.16 in 2007, 129 ± 20.24 in 2008), and it will likely play a role in the possible recovery of the population. While a slight increase in length-at-age is sufficient to dramatically increase (scenario DI+5%) or decrease (scenario DI-5%) the number of eggs produced, the mean per-capita egg production 4 years after a population collapse caused by a flood event is greater in the DD scenario (Fig. 2c) than in any of the DI cases analysed in this study. These results suggest that slight changes in individual growth at low population densities allow an increase in recruitment

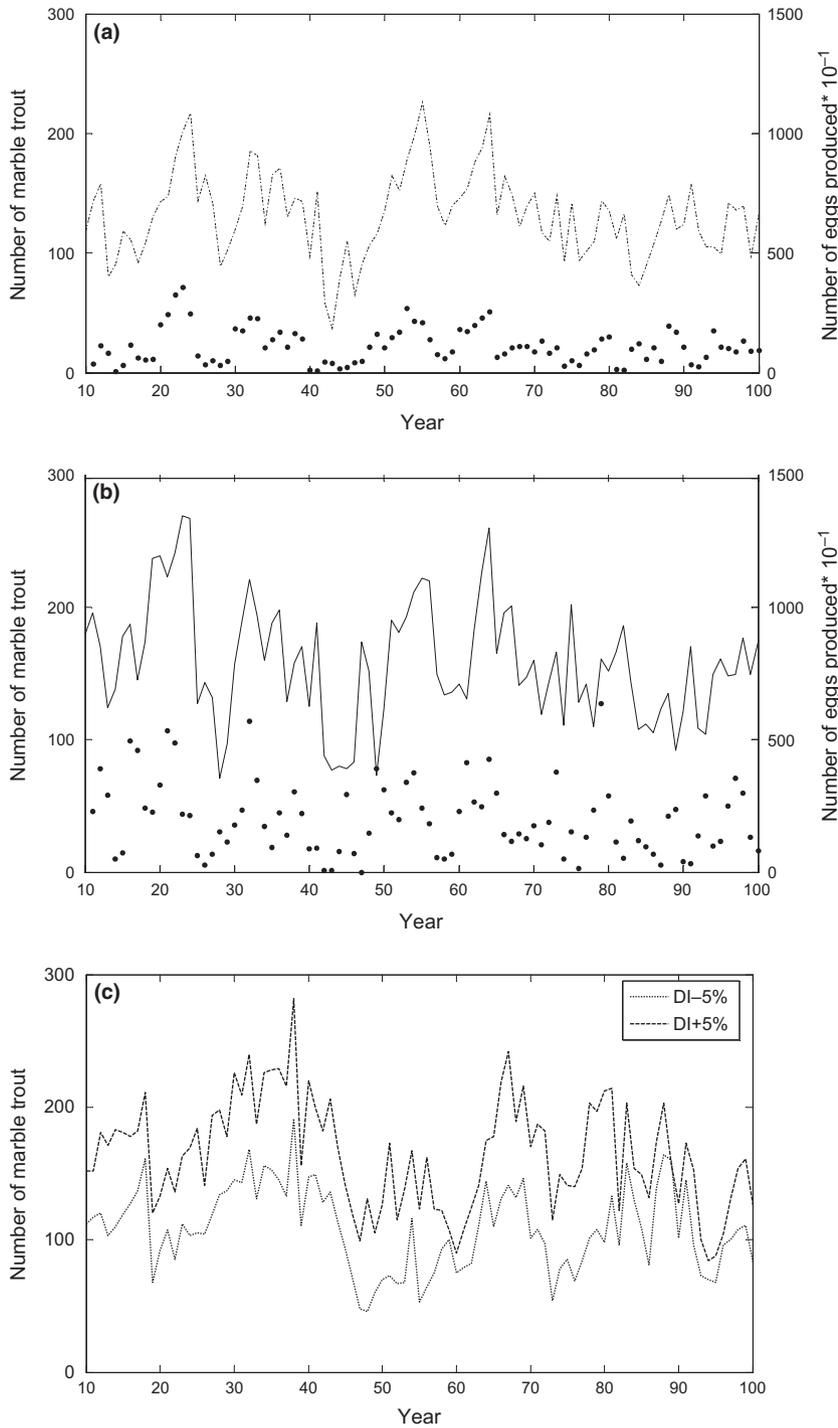


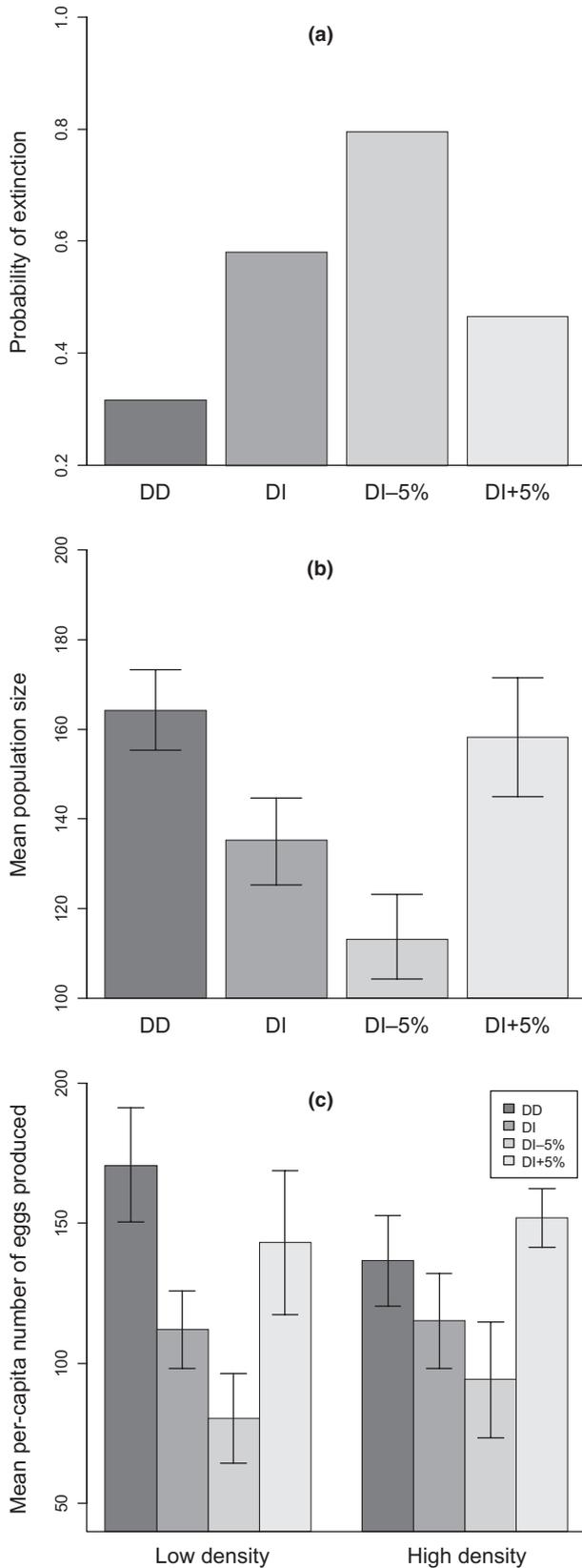
Fig. 1. Sample trajectories of population dynamics of marble trout with different model assumptions: (a) Von Bertalanffy growth scenario (DI); (b) density-dependent growth scenario (DD); (c) Von Bertalanffy growth scenarios with $\pm 5\%$ change in mean length-at-age ($DI \pm 5\%$). In (a) and (b) panels the number of eggs produced is also shown (●).

sufficient to reduce the risk of extinction and rapidly re-establish pre-event population size.

Jenkins et al. (1999) pointed out that high individual growth rates at low densities may theoretically enable stream-dwelling salmonid populations to rebound quickly after catastrophic density-independent mortality events, such as extreme floods caused by snow-melt peaks or ice dams dewatering stream reaches, through an increase in egg production and a relaxation of density-dependent early survival. Also, in an Atlantic

salmon population living in the Sawmill River, a localised massive flood event provided greater growth opportunities for the surviving individuals by drastically reducing competitors. The relaxed intra-specific pressure induced higher maturation rates (74% of 0+ individuals mature the year after the flood vs. 5% before the flood) leading to a fast recovery of the population to pre-event levels (Letcher & Terrick 1998).

While it is intuitive that large variations in body size may have a substantial effect on fecundity and



population size, here we showed that even slight variations in mean body growth trajectories were sufficient to remarkably increase or decrease (scenario

Fig. 2. (a) Probability of extinction for the population of Zakojska in four simulation scenarios, namely: DD, density-dependent individual growth; DI, growth predicted by the density-independent Von Bertalanffy growth curve; DI-5%, as scenario DI, with length-at-age decreased by 5%; DI+5%, as scenario DI, with length-at-age increased by 5%; (b) Mean population abundance across replicates (\pm SD) and (c) mean per-capita egg production across replicates (\pm SD) at high density (high density, population size ≥ 200 ind., density ≥ 0.22 ind·m⁻²) and 4 years after the occurrence of a severe flood event (low density, population size ≤ 70 ind., density ≤ 0.08 ind·m⁻²), when the cohort experiencing a very low density during the first year of life spawns for the first time.

DI+5% and scenario DI-5%, respectively) the risk of extinction (Fig. 2), mean population abundance, and mean per-capita egg production with respect to scenarios DI and DD (Figs 1 and 2). This means that while density-dependent first-year survival has undoubtedly a strong role in regulating population size (Vincenzi et al. 2008a), i.e., to prevent a population from growing unbounded, even slight variations in the growth pattern of fish such as those occurring after a drop in population size caused by exogenous events may influence reproductive output and population size (Fig. 2c). Evidence of compensatory recruitment induced by density-dependent growth has been found also in marine environment (e.g., haddock on the southwest Scotian Shelf in the North Atlantic, Marshall & Frank 1999). Periodic surveys revealed a negative relationship between mean length at age 1 and adult abundance with differences in mean body length persisting through the adult stage. Moreover, recruitment was positively related to the mean length of adults, thus possibly leading to the cyclic population behaviour observed in a variety of stocks due to the following negative feedback on recruitment: high adult abundance leads to short mean length at age 1 causing short mean length 3 years later (i.e., at age 4), leading to low reproductive output the next year and, again, to low adult abundance three years later.

Our simulation analysis revealed an important role of the carry-over effect of early density on body growth. Carry-over effects have been observed in fishes, although their role have been rarely integrated in model population dynamics and deserves further investigation. In an interesting experiment on the cichlid fish *Simochromis pleurospilu*, Taborsky (2006) found that juvenile growth exhibits carry-over effects on reproductive behaviour, investment in offspring and key life-history trade-offs. Fleming et al. (1997) showed in an experimental setting the long-lasting effect of early experience in Atlantic salmon. Fish with a common genetic background reared as juveniles either naturally in the river or artificially in a hatchery (sea ranched), and then allowed to grow to maturity naturally in the ocean, showed different reproductive performance at maturity, with wild individuals

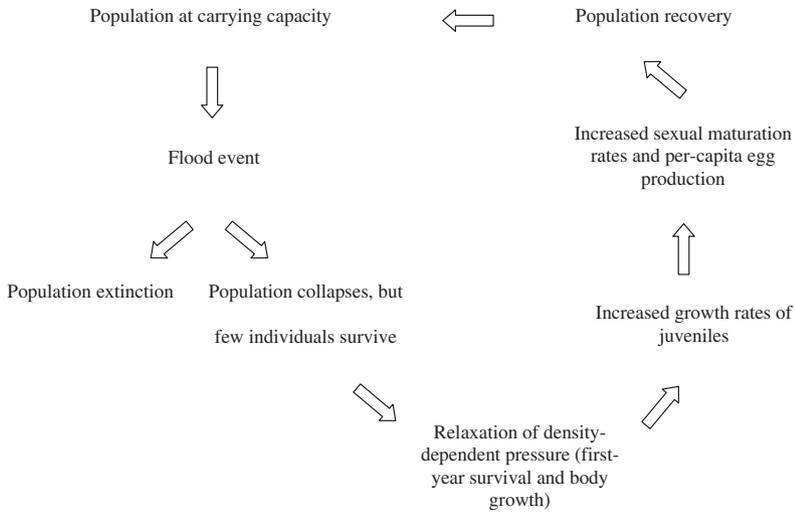


Fig. 3. Occurrence of a severe flood event, increase of individual body growth rates and consequent recruitment dynamics in marble trout. The relaxation of density-dependent first year survival and density-dependent growth increases recruitment in the years following the population collapse.

displaying higher the better reproductive performances. Fleming et al. (1997) concluded that early experience affects the development of specialised skills and traits important also for later life. Jonsson et al. (1996) reported that juvenile growth explained part of the variation in number of eggs produced by Atlantic salmon. For brown trout, Lobón-Cerviá et al. (1997) found that the number of eggs produced by females aged 1+ was determined when trout were still 0+ (Esva River, Spain). Lobón-Cerviá (2005) found a negative power relationship between initial cohort size and lifetime growth in weight of the same cohort (Rio Chaballos, Spain). Alvarez et al. (2006) found that temperature during the yolk-absorptive stage can shape the evolution of metabolic rate and later growth performance in brown trout.

The analyses performed in the present work are based on a demographic model with parameters calibrated on the data available for marble trout in Zakojska, Slovenia. Some of model parameters – such as a linear relationship between body length and number of eggs produced or the absence of maternal effect on egg size – represent observed patterns for the marble trout population of Zakojska, but due to local adaptations those patterns may be slightly different even in other marble trout populations living in the same general region. In several salmonids, the number of eggs produced increases linearly or more than linearly with body weight which, in turn is almost ubiquitously proportional to the cube of body length (Wootton 1998). In addition, it has been observed that larger females may also produce larger and more viable eggs (Wootton 1998). We thus wondered whether our conclusions on the role of density-dependent body size would still hold true in the case of alternative assumptions on the relationship between length and number of eggs produced and maternal effect on eggs survival. Accordingly, we ran further

simulations for hypothetical marble trout populations in which – all the other parameters being equal – the relationship between body length and per capita egg production is a power curve with exponent close to three (Wootton 1998), or egg survival is slightly greater for larger females. The alternative model parameters were tuned to provide the same population size at quasi-stable equilibrium in the absence of environmental variability, i.e., about 270 individuals. Results of the simulations (not reported here) under variable environment with a power curve relationship between length of female and fecundity or maternal effects on eggs survival are consistent with the main conclusions of the present work, i.e., that density-dependent individual growth increases resilience to flood events and helps regulate recruitment in marble trout in recruitment dynamics.

In the marble trout of Zakojska, we did not find strong evidence in favour of compensatory body growth after the first year of life, but its role in the recruitment dynamics deserves further investigations. In fact, while compensatory body growth was scarcely observed in marble trout, taxonomically close species may have different propensities to show compensatory responses (Ali et al. 2003). In addition, the costs and benefits of fast growth may be context-dependent, including effects of previous growth history, i.e., how quickly individuals have grown in the past (Carlson et al. 2004). Selection on growth may also depend on the overall pattern of growth in the population. In general, compensatory growth may require more risky foraging strategies and increase the mortality of small individuals growing fast (Damsgard & Dill 1998), but in a population of brown trout, Carlson et al. (2004) found that mortality decreased for individuals exhibiting fast growth, thus reinforcing the context- and species-dependent propensity to show compensatory growth later in life.

Obviously, other factors contribute to regulating and influencing population size in stream-dwelling salmonids and thus limit the generality of the results of our simulation analysis. A reduction in cannibalism may in part explain the spike in juveniles commonly observed after severe flood events in salmonid populations. It is generally recognised that cannibalism may contribute to stabilisation population numbers (Dong & Polis 1992) and alter size distributions (Crowley & Hopper 1994). In marble trout cannibalism has been observed (Dusan Jesensek, personal communication) and further investigation is needed to assess its role in marble trout recruitment dynamics. Environmental factors such as stream discharge can modify suitable habitat for fish and alter spawning grounds and thus influence the overall reproductive output and population size (Lobón-Cerviá & Rincon 2004). The striking contrast of closely related salmonid species in age and size at maturity, semelparity versus iteroparity, egg size versus number, shape of size-fecundity relationship, life-histories and breeding tactics (Hendry & Stearns 2004) may hinder generalisations on the implications of density-dependent individual growth on compensatory recruitment. Further observational data that will be available in the future for other marble populations living in the same region will be used to extensively validate model results. Moreover, it will be worth investigating the consequences of different trade-offs between mortality and body growth in density-dependent growth scenario. While density-dependent early survival is generally recognised as an important mechanism of population regulation and the role of environmental factors in influencing population size is widely acknowledged, further investigations on the implications of density-dependent individual growth in population dynamics are greatly encouraged.

Acknowledgements

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

References

- Ali, M., Nicieza, A. & Wootton, R.J. 2003. Compensatory growth in fishes: a response to growth depression. *Fish & Fisheries* 4: 147–190.
- Alvarez, D., Cano, J.M. & Nicieza, A.G. 2006. Microgeographic variation in metabolic rate and energy storage of brown trout: countergradient selection or thermal sensitivity? *Evolutionary Ecology* 20: 345–363.
- Beverton, R.J.H. 2002. Fish population biology and fisheries research. In: Anderson, E.D., ed. *The Raymond J. H. Beverton Lectures at Woods Hole*. Massachusetts: U.S. Department of Commerce, pp. 61–106. NOAA Tech. Memo. NMFS-F/SPO-5.
- Beverton, R.J.H. & Holt, S.J. 1957. *On the dynamics of exploited fish populations*. London: Chapman & Hall.
- Carlson, S.M., Hendry, A.P. & Letcher, B.H. 2004. Natural selection acting on body size, growth rate and compensatory growth: an empirical test in a wild trout population. *Evolutionary Ecology Research* 6: 955–973.
- Crowley, P.H. & Hopper, K.R. 1994. How to behave around cannibals: a density-dependent dynamic game. *American Naturalist* 143: 117–154.
- Damsgard, B. & Dill, L.M. 1998. Risk-taking behavior in weight-compensating coho salmon, *Oncorhynchus kisutch*. *Behavioral Ecology* 9: 26–32.
- Dong, Q. & Polis, G.A. 1992. The dynamics of cannibalistic populations: a foraging perspective. In: Elgar, M.A. & Crespi, B.J., eds. *Cannibalism: ecology and evolution among diverse taxa*. Oxford: Oxford University Press, pp. 13–37.
- Elliott, J.A. 1994. *Quantitative ecology and the brown trout*. Oxford: Oxford University Press.
- Fleming, I.A., Lamberg, A. & Jonsson, B. 1997. Effects of early experience on the reproductive performance of Atlantic salmon. *Behavioral Ecology* 8: 470–480.
- Grant, J.W.A. & Imre, I. 2005. Patterns of density-dependent growth in juvenile stream-dwelling salmonids. *Journal of Fish Biology* 67: 100–110.
- Hendry, A.P. & Stearns, S.C. (eds.) 2004. *Evolution illuminated: Salmon and their relatives*. Oxford: Oxford University Press.
- Hutchings, J.A. 2003. Life histories of fish. In: Hart, P.J.B. & Reynolds, J.D., eds. *Handbook of fish biology and fisheries*. Vol. 1. Fish Biology. Oxford: Blackwell Science, pp. 149–174.
- Imre, I., Grant, J.W.A. & Cunjack, 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.
- 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.
- Jonsson, N., Jonsson, B. & Fleming, I.A. 1996. Does early growth cause a phenotypically plastic response of egg production to early growth in Atlantic salmon? *Functional Ecology* 10: 89–96.
- Kozłowski, J. 2006. Why life histories are diverse. *Polish Journal of Ecology*, 54: 585–605.
- Letcher, B.H. & Terrick, T.D. 1998. Maturation of male age-0 Atlantic salmon following a massive, localized flood. *Journal of Fish Biology* 53: 1243–1252.
- Lindstrom, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology and Evolution* 14: 343–348.
- Lobón-Cerviá, J. 2005. The importance of recruitment for the production dynamics of stream-dwelling brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* 62: 2484–2493.
- Lobón-Cerviá, J. 2007. Density-dependent growth in stream-living Brown Trout *Salmo trutta* L. *Functional Ecology* 21: 117–124.
- Lobón-Cerviá, J. & Rincon, P.A. 2004. Environmental determinants of recruitment and their influence on the population

- dynamics of stream-living brown trout *Salmo trutta*. *Oikos* 105: 641–646.
- Lobón-Cerviá, 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.
- Lorenzen, K. 2008. Fish population regulation beyond ‘stock and recruitment’: the role of density-dependent growth in the recruited stock. *Bulletin of Marine Science* 83: 191–196.
- Marshall, C.T. & Frank, K.T. 1999. Implications of density-dependent juvenile growth for compensatory recruitment regulation of haddock. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 356–363.
- Meldgaard, T., Crivelli, A.J., Jesensek, D., Poizat, G., Rubin, J.F. & Berrebi, P. 2007. Hybridization mechanisms between the endangered marble trout (*Salmo marmoratus*) and the brown trout (*Salmo trutta*) as revealed by in-stream experiments. *Biological Conservation* 136: 602–611.
- 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.
- Rochet, M.J. 1998. Short-term effects of fishing on life history traits of fishes. *ICES Journal of Marine Science* 55: 371–391.
- Rose, K.A., Cowan, J.H., Winemiller, K.O., Myers, R.A. & Hilborn, R. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* 2: 293–327.
- Schlichting, C.D. & Pigliucci, M. 1998. Phenotypic evolution: a reaction norm perspective. Sunderland: Sinauer Associates.
- Taborsky, B. 2006. The influence of juvenile and adult environments on life-history trajectories. *Proceedings of the Royal Society of London B* 273: 741–750.
- Turchin, P. 1995. Population regulation: old arguments and a new synthesis. In: Cappuccino, N. & Price, P.W., eds. *Population dynamics: novel approaches and synthesis*. San Diego: Academic Press, pp. 19–40.
- Utz, R.M. & Hartman, K.J. 2009. Density-dependent individual growth and size dynamics of central Appalachian brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 66: 1072–1080.
- Vincenzi, S., Crivelli, A.J., Jesensek, D., Rubin, J.-F. & De Leo, G.A. 2007a. Early survival of marble trout *Salmo marmoratus*: evidence for density dependence? *Ecology of Freshwater Fish* 16: 116–123.
- Vincenzi, S., Crivelli, A.J., Jesensek, D., Rubin, J.-F. & De Leo, G.A. 2007b. 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.J., Jesensek, D. & De Leo, G.A. 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., Rubin, J.-F., Poizat, G. & De Leo, G.A. 2008c. Potential factors controlling the population viability of newly introduced endangered marble trout populations. *Biological Conservation* 141: 198–210.
- 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.
- White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation for population of marked animals. *Bird Study* 46: 120–139.
- Wootton, R.J. 1998. *Ecology of teleost fishes*. Fish and Fisheries Series 24. London: Kluwer Academic Publishers.