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The role of density-dependent individual growth in the persistence of freshwater salmonid populations

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Abstract Theoretical and empirical models of populations dynamics have paid little attention to the implications of density-dependent individual growth on the persistence and regulation of small freshwater salmonid populations. We have therefore designed a study aimed at testing our hypothesis that density-dependent individual growth is a process that enhances population recovery and reduces extinction risk in salmonid populations in a variable environment subject to disturbance events. This hypothesis was tested in two newly introduced marble trout (*Salmo marmoratus*) populations living in Slovenian streams (Zakojska and Gorska) subject to severe autumn floods. We developed a discrete-time stochastic individual-based model of population dynamics for each population with demographic parameters and compensatory responses tightly calibrated on data from individually tagged marble trout. The occurrence of severe flood events causing population collapses was explicitly accounted for in the model. We used the model in a population viability analysis setting to estimate the quasi-extinction risk and demographic indexes of the two marble trout populations when individual growth was density-dependent. We ran a set of simulations in which the effect of floods on population abundance was explicitly accounted for and another set of simulations in which flood events were not included in the model. These simulation results were compared with those of scenarios in which individual growth was modelled with density-independent Von Bertalanffy growth curves. Our results show how density-dependent individual growth may confer remarkable resilience to marble trout populations in case of major flood events. The resilience to flood events shown by the simulation results can be explained by the increase in size-dependent fecundity as a consequence of the drop in population size after a severe flood, which allows the population to quickly recover to the pre-event conditions. Our results suggest that density-dependent individual growth plays a potentially powerful role in the persistence of freshwater salmonids living in streams subject to recurrent yet unpredictable flood events.

Keywords Compensatory responses · Flood disturbance · Marble trout · Population dynamics · Resilience

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Introduction

Understanding regulatory processes is essential for a successful management of endangered populations (Hixon et al. 2002). However, density-dependence is often ignored by the conservation biologist because

threatened populations are usually small relative to historical levels and are therefore assumed to be immune to compensatory patterns associated with intra-specific competition (Achord et al. 2003). 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 (Rose et al. 2001). An approach integrating life-history theory, process-level understanding of mechanisms, analysis of field data and individual-based modelling is suggested.

Stream-dwelling salmonids are good candidates for investigating the relative contributions of endogenous and exogenous factors in population regulation. Freshwater salmonids are commonly subject to substantial environmental variability in the form of changes in mean stream flow at different time scales and extreme events, such as floods and droughts (Grossman et al. 1982, 1998; Lake 2000). In addition, density-dependent effects on population dynamics have been widely observed in freshwater salmonids species (e.g. Rose et al. 2001). Detailed knowledge of the biology and ecology of salmonids and a wealth of theoretical and empirical evidence (e.g. Elliott 1993, 1994; Cattaneo et al. 2002) suggest the crucial importance of endogenous mechanisms in regulating population dynamics of salmonids—especially in stable systems where abiotic influences are rare—although a quantification of the relative importance of density-dependent factors versus exogenous factors is still lacking (Lobon-Cervia and Rincon 2004; Einum 2005). While the support for a density-dependent regulation of abundance in stream-dwelling salmonids through newborn mortality is overwhelming (Milner et al. 2003), both theoretical and empirical models of population dynamics of stream-dwelling salmonids have rarely considered the implication of density-dependent growth in population dynamics (Milner et al. 2003). Consequently, the potential role of density-dependent individual growth in population regulation and persistence remains little appreciated (Lorenzen and Enberg 2002) and is still controversial (e.g. Rose et al. 2001). A key question addressed here is: to what extent and under which conditions may the effects of density on individual growth influence population size and possibly increase its persistence?

Theoretically, the direct impact of density on individual growth can potentially have dramatic consequences on the demography and persistence of stream-dwelling salmonids through a cascade of secondary effects on fecundity and on age and length at sexual maturity (e.g., Rose et al. 2001). In fact, a tight relationship linking female length to sexual maturity and egg production is commonly observed in salmonids (e.g., Koops et al. 2004). Moreover, a number of studies on salmonid species have reported a general correlation between rapid growth and early sexual maturation (Hutchings and Jones 1998; Utrilla and Lobón-Cerviá 1999); therefore, slowly growing individuals may delay sexual maturation in order to reach the minimum size required for gonad development. Several authors have proposed examples of changes in fecundity that could provide a compensatory mechanism serving to stabilize fish populations (Nikolsky 1969; Nikolsky et al. 1973; Rothschild and 1989). However, other authors have expressed doubts that density-dependent changes in adult growth affecting fecundity and sexual maturation can stabilize recruitment (e.g., Craig and Kipling 1983; Koslow 1992). Following a major disturbance, such as a severe flood, the decreased density of the fish population combined with an increased food supply creates the potential for the increased growth of the individuals recolonizing the impacted areas (Sousa 1984). This phenomenon has been observed in salmonid populations (Lennon 1961; Elwood and Waters 1969; Lamberti et al. 1991; Swanson 1998). Moreover, Letcher and Terrick (1998) reported that flood events causing drastic reductions in population size may trigger faster individual growth rates in freshwater salmonids that in turn are related to higher maturation rates and egg production.

Our hypothesis is that density-dependent individual growth is a process that enhances population recovery and reduces the extinction risk of stream-dwelling salmonid populations in a variable environment subject to disturbance events, such as floods. We have tested this hypothesis in two newly introduced populations of marble trout (*Salmo marmoratus*) in the Soca and Idrjica river basins (Slovenia). Major floods are probably the most important risk factor for the viability of marble trout populations living in Slovenian streams (Vincenzi et al. 2008). Ten years of data from individually tagged marble trout enabled us to estimate the main life-history traits of these populations, i.e. age-specific survival, body-size growth rates and the relationship between female length and fecundity (Vincenzi et al. 2007a, b, 2008). We also observed density-dependent patterns in marble trout for both individual growth (Vincenzi et al. 2007b) and first-year survival (Vincenzi et al. 2007a). Here, we report our individual-based model of marble trout population dynamics which we developed based on marble trout population parameters and empirical models of density-dependent processes (Vincenzi et al. 2007a, b, 2008). We also used a population viability analysis (PVA) approach (Morris and Doak 2002) to compare population dynamics, risk of extinction and measures of population performance under alternative assumptions on individual growth and on the magnitude and effect of disturbance events.

Materials and methods

Study area and species description

Marble trout is an endangered species with a limited geographic distribution in the basin of Po river in Northern Italy (Sommani 1961; Forneris et al. 1990), in the Adriatic basin of Slovenia (Povz et al. 1996) and in Albania (Schoffmann 1994). Presently, only seven remnant pure (i.e. non-hybrid, Berrebi et al. 2000; Fumagalli et al. 2002) marble trout populations are located in the Adriatic basin of Slovenia (Crivelli et al. 2000; Fumagalli et al. 2002). The remnant populations persist in isolated headwaters in Slovenia with natural barriers (i.e. waterfalls) preventing upstream movement. Therefore, there is no potential for spontaneous colonization of new habitats or re-colonization after local extinctions. To enhance species viability, a conservation programme was launched in 1993 (Crivelli et al. 2000) to duplicate the existing pure populations. Two new translocated marble trout populations were created in 1996 in previously fishless streams in the study area (Zakojska and Gorska) by stocking 500 individuals of marble trout aged 1+. The trout of these two populations share the same genetic background. Since 1996, an annual monitoring programme has been carried out to assess the long-term persistence, life-history traits, compensatory responses and population dynamics of those new populations. Marble trout is the only fish species present in both the experimental streams (Gorska and Zakojska), both populations are located in headwaters and there is no predation or fishing activities. Immigration of marble trout is prevented by natural barriers (i.e., waterfalls). The stream bed of Gorska consists mostly of bedrock slides, with few shelter areas and a minimal floodplain. In contrast, Zakojska has a wider stream bed and at times of flooding, it can overflow its bank, potentially creating new suitable habitat for marble trout on a wide area of riparian forest. Both mean population size and density from 2000—when the first cohort of marble trout hatched within the streams—to 2004 were higher in Zakojska (no. of marble trout 284.61 ± 72.27 ind.; density 0.31 ± 0.08 ind. m^{-2}) than in Gorska (no. of marble trout 90.42 ± 34.04 ind.; density 0.13 ± 0.05 ind. m^{-2}). The annual mean precipitation from 1961 to 2004 was 2400 mm, with October and November presenting the highest monthly precipitation (ARSO, Environmental Agency of Slovenia). Annual rainfall for the study period varied little across years, ranging from 1764.5 mm in 2003 to 2495.7 of 2000. The water temperature of the streams was recorded with temperature loggers (Optic Stoneway model; Onset Corp, Bourne, MA) at hourly intervals. The annual average water temperature during the study period in Gorska and in Zakojska varied between 8.2 and 9.0°C and 7.6 and 8.2°C, respectively.

In the study area, maximum age recorded for marble trout was 6 years. Marble trout feed generally on bottom-dwelling organisms, with some evidence of cannibalism. Spawning takes place in November–December, with marble trout eggs generally hatching in March and emergence occurring in April–May. Observational data in the Soca and Idrijca river basins where pure marble trout occur showed evidence of multiple reproduction events (iteroparity).

Detailed descriptions of the study area, surveys and the statistical methods used to estimate the demographic traits and compensatory responses of marble trout living in Slovenian streams have been provided elsewhere (Vincenzi et al. 2007a, b). Therefore, only those aspects relevant to this study are described here.

Demographic parameters of marble trout

Information on the demographic traits of marble trout were obtained from the tag–recapture monitoring of the translocated population from 1996 to 2004. The annual survival rate of marble trout hatched in Zakojska and Gorska aged $\geq 1+$ σ_A was estimated separately for each stream using the Cormack–Jolly–Seber method. Estimates of σ_A along with 95% confidence intervals are provided in Table 1 (Vincenzi et al. 2008). Size-dependent survival was tested using a generalized linear model (GLM; McCullagh and Nelder 1989) at age $1+ \cdots 4+$ (we did not have enough data for 5+ individuals). Length and weight of marble trout did not predict survival at any age (GLM, $P > 0.05$ for all ages).

As reported by Vincenzi et al. (2007a), the number of eggs produced E was related to total length L_T of female by the linear relationship:

$$E = \alpha + \beta L_T \tag{1}$$

Model parameters are reported in Table 1.

Parental analyses performed on marble trout populations living in the study area showed a minimum (3+) and maximum (5+) spawning age for marble trout females (Meldgaard et al. 2007). 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).

Density-dependent survival

In salmonids, density-dependent effects on mortality act mostly during the very early stages of life (30–70 days after hatching; Elliot 1993), after which mortality is density-independent. Vincenzi et al. (2007a) found a significant effect of egg density (E_D) on survival from eggs to age 1+ (σ_0) in marble trout living in Gorska and

Table 1 Parameters of the individual-based model of population dynamics for the Gorska and Zakojska marble trout populations

Parameter	Zakojska		Gorska		Description
	Experimental value	95% CI	Experimental value	95% CI	
a	8.67	8.60–8.74	0.50	0.45–0.55	Parameters of the density-dependent first-year survival function
γ	0.68	0.66–0.70	0.38	0.36–0.42	
σ_A	0.57	0.53–0.62	0.61	0.57–0.65	Adult survival
α	−749.97	−944.68 to −525.26	−749.97	−944.68 to −525.26	Parameters of the linear model of egg production
β	3.8	2.45–5.15	3.8	2.45–5.15	
L_∞	318.24	294.69–351.27	376.76	345.75–418.66	Parameters of the Von Bertalanffy growth function
k	0.34	0.27–0.41	0.31	0.25–0.36	
x_0	−0.34	−0.49 to −0.20	−0.33	−0.40 to −0.26	
β_{DU}	0.01	−0.09–0.10	−0.57	1.04 to −0.09	Parameters of the models of density-dependent individual growth
β_{Dx}	−0.18	−0.33 to −0.04	−1.24	−1.87 to −0.60	
β_L	−0.001	−0.001 to −0.0008	−0.001	−0.002 to −0.0008	
β_{1+}	0.56	0.50–0.62	0.75	0.64–0.87	
β_{2+}	0.43	0.35–0.50	0.70	0.56–0.84	
β_{3+}	0.40	0.32–0.49	0.67	0.50–0.83	
β_{4+}	0.3	0.20–0.40	0.67	0.50–0.83	
β_{5+}	0.3	0.20–0.40	0.67	0.50–0.83	
c_{1+}	100.70	92.37–109.52	100.70	92.37–109.52	
c_{2+}	143.44	124.38–164.22	143.44	124.38–164.22	
c_{3+}	177.82	137.30–225.61	177.82	137.30–225.61	
c_{4+}	204.36	144.04–280.32	204.36	144.04–280.32	
δ_{1+}	−0.11	−0.16 to −0.06	−0.11	−0.16 to −0.06	
δ_{2+}	−0.16	−0.23 to −0.09	−0.16	−0.23 to −0.09	
δ_{3+}	−0.15	−0.27 to −0.03	−0.15	−0.27 to −0.03	
δ_{4+}	−0.14	−0.28 to −0.04	−0.14	−0.28 to −0.04	

95% CI, 95% Confidence interval

Zakojska. The relationship was modelled with a negative power law curve in the form:

$$\sigma_0 = aE_D^{-\gamma} \qquad (2)$$

Estimates of a and γ along with their respective 95% confidence intervals (CI) for Zakojska and Gorska marble trout populations are reported in Table 1. No evidence of density-dependent mortality was found for marble trout aged >1+ (Vincenzi et al. 2007a).

Density-dependent individual growth

Individual growth was modelled using density-independent Von Bertalanffy growth curves in the form:

$$L_x = L_\infty \left(1 - \exp(-k(x - x_o))\right) \qquad (3)$$

where x is the age (years), L_∞ is the maximum length (mm), k is the Brody's growth coefficient relating age to length and x_0 (years) is the age at which length equals 0. The growth curve parameters for both Gorska and Zakojska marble trout populations were estimated separately by pooling together age–length data from different years (Vincenzi et al. 2007b) (Table 1). However, Vincenzi et al. (2007b) found evidence of density-dependent individual growth in the newly introduced marble trout populations. A number of factors have been suggested to explain the phenomenon of density-dependent growth in freshwater salmonids; these range from overcrowding to low food availability and thus constrained feeding rates (Klemetsen et al. 2003) and increased defence costs (Hixon 1980). A recent meta-analysis on density-dependent growth in juvenile stream-dwelling salmonids (Grant and Imre 2005) suggested that population density affects individual growth via exploitative competition—that is the depletion of food by competitors (Keddy 1989). In this context, low growth rates are viewed as plastic phenotypic responses to low food availability. By pooling the stream-specific data sets of the newly introduced populations, the mean length of the individuals of a cohort at age 1+ ⋯ 4+ ($\bar{L}_{1+} \cdots \bar{L}_{4+}$) was negatively correlated with total density of marble trout aged ≥1+ when the cohort was in its first year of life (D_U, density as underyearlings), with the relationship described

by age-specific negative power curves in the form (Vincenzi et al. 2007b):

$$\bar{L}_x = c_x D_U^{-\delta_x} \quad x = 1 + \cdots 4+ \tag{4}$$

Total density of marble trout aged $\geq 1+$ was estimated by dividing the number of marble trout aged $\geq 1+$ by the overall surface area of pools (Zakojska 895 m^2; Gorska 685 m^2), as it offered the best quantification of instream suitable habitat for marble trout.

Individual growth rates

$$\left(G_{Lx} = \ln\left(\frac{L(x+1)}{L(x)}\right) x = 1 + \cdots 4 + \right)$$

were well described by the linear model:

$$G_{Lx} = \beta_x x + \beta_{D_u} D_U + B_{L_T} L_T + \beta_{D_x} D_x \tag{5}$$

where x is the age of marble trout (categorical variable) and D_x is the total density of marble trout aged $\geq 1+$ when the marble trout is aged x (Vincenzi et al. 2007b). The parameters of linear models (4) and (5) are reported in Table 1.

Environmental factors

Many studies suggest an important role of floods and droughts in the regulation of freshwater salmonid populations (Elliott et al. 1997; Jensen and Johnsen 1999; Weng et al. 2001). Moreover, Roghair et al. (2002) suggested that in high-gradient streams, fish populations are to a large extent shaped by extreme flow events. The direct and short-term effects of floods are largely a result of high-water velocities and sediment movement that cause the displacement and death of fish. The impact of floods on fish survival appears to vary widely and may depend on the complexity of the habitat (Lobon-Cervia 1996), severity (Seegrist and Gard 1972) and timing of the flood, relative susceptibility of the different life stages (Seegrist and Gard 1972; Hansen et al. 1989) and the species involved (Harrell 1978). By examining the population dynamics of *Salmo trutta* L. and hydrological features over 5–8 years in 30 French streams, Cattaneo et al. (2002) found that the discharge pattern played an important role in regulating population size. *Salmo marmoratus* populations living in Slovenian streams are heavily affected by the hydrological regime and, in particular, by severe floods in the autumn season. This was confirmed when a severe flood in October 2004 with a recurrence interval of 50–100 years—which took the form of a debris flow in Gorska—wiped out the whole population of Gorska and caused a remarkable reduction of population size in several marble trout populations in the study area (Fig. 1). In contrast, stream discharge during emergence did not affect first-year survival of marble trout living in the two
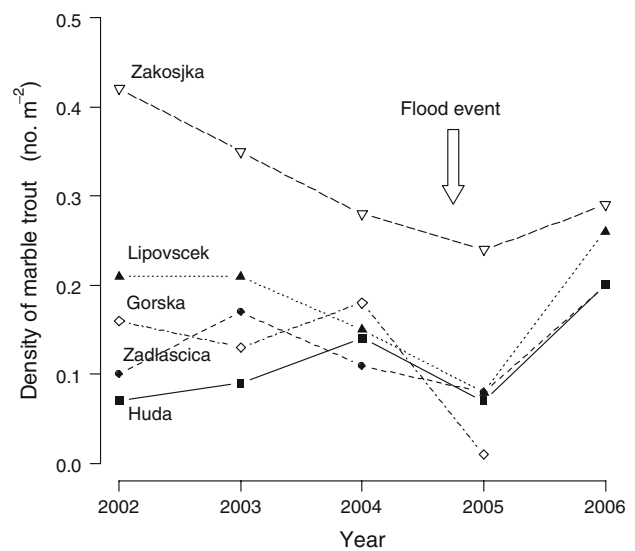
Fig. 1 Population size (no. m^{-2}) of marble trout (*Salmo marmoratus*) 1 year or older in three remnant populations (Zadlascica, Lipovscek, Huda) and in two experimental populations (Zakojska and Gorska) living in the study area from 2002 to 2006, before and after the October 2004 flood. As sampling surveys were carried out in June, the most immediate effect of the October 2004 flood was observed in the population densities of June 2005. The Gorska population was completely obliterated by a debris flow occurring in October 2004 provoked by the same flood event

experimental streams prior to the flood of October 2004 (Vincenzi et al. 2007a).

Catastrophic events quickly decrease the size of a population and could have caused the majority of local extinction of freshwater salmonids. Even when the distribution of catastrophic events is unknown, in PVA settings it is sensible to model the potential impact of catastrophes on the studied population (Coulson et al. 2001). In our case, the effects of floods on population abundance were modelled as described hereafter. Floods occur primarily in October in the study area. As quantitative data on stream discharge were not available, rainfall data in October (ARSO, Environmental Agency of Slovenia) were used as a proxy-indicator of flood events. The effect of floods on population abundance was described through a simple non-linear fuzzy function linking October rainfall to a flood-induced mortality factor F, indicating the reduction in population size induced by a flood event, ranging between 0 for low discharges to F_{max} for major flood events. A log-normal distribution was fitted to the October rainfall data from 1961 to 2004 ($\mu = 5.36 \pm 0.13$, $\sigma = 0.89 \pm 0.09$). We assumed that flood effects are negligible when rainfall is below the 15th percentile of the lognormal distribution of the October rainfall data, equal to F_{max} for rainfall exceeding the 85th percentile and increase linearly from 0 to F_{max} when rainfall is intermediate. F_{max} was set to 0.7—meaning a 70% reduction in population size—which is

equivalent to the maximum decrease in population size observed in marble trout populations living in the study area (remnant and translocated) after the October 2004 flood (Fig. 2). As the choice of F_{max} is debatable, we ran a sensitivity analysis of the simulation results for values of F_{max} ranging from 0.6 to 0.8.

Even though the same rainfall pattern can result in different reductions in population size in Gorska and Zakojska due to stream morphology and the presence of the flood plain, we did not consider any difference in flood dynamics between the two streams. We also assumed that suitable habitat for marble trout within the streams remains unaffected by flood events.

The individual-based model

We designed an individual-based model with a time step of 1 year incorporating the compensatory responses observed in marble trout populations and the occurrence of flood events. As already described, demographic parameters were estimated on the basis of the data available for the two marble trout populations of Gorska and Zakojska, respectively. As marble trout is the only fish species living in Gorska and Zakojska, we did not consider any inter-specific interactions. Our individual-based model allowed us to track the age and size of each individual in the population and to follow its demographic fate. The model included both demographic and environmental stochasticity. Environmental stochasticity refers to variations in birth and death rates in response to environmental factors, such as water temperature, food availability and disease. Environmental stochasticity was incorporated in the model by drawing—for each year—a random deviate for each demographic parameter from the corresponding probability distribution function reported in Table 1. Demographic
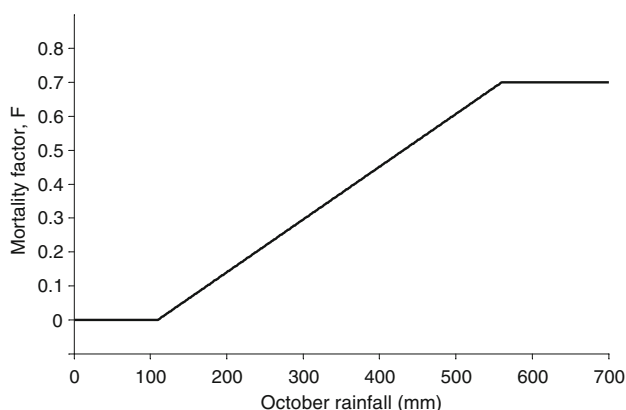
Fig. 2 Non-linear fuzzy function linking the mean of October rainfall to the flood-induced mortality factor F

stochasticity refers to the variability in survival and reproduction arising from random differences among individuals, even when all the individuals share the same expected probability. In the present study, given the expected age-specific survival, demographic stochasticity was simulated by randomly drawing for each individual a random deviate from a uniform distribution: if the deviate was smaller than the corresponding probability value, the individual was assumed to survive until the following year; otherwise, it was assumed to die.

We designed the model so as to explore the demographic consequences of two alternative hypotheses: in the first case, we assumed that age-specific individual growth of marble trout was affected by population density, as shown by Vincenzi et al. (2007b). This scenario will be referred to as density-dependent (DD)-growth scenario hereafter. In the second case, we assumed that age-specific individual growth of marble trout was not affected by population density. Therefore, the individual length at age x was computed by applying the Von Bertalanffy growth function (Eq. 3) estimated for Gorska and Zakojska, separately (Table 1). We refer to this case as the VB-growth scenario.

As we hypothesized that density-dependent individual growth enhances population resilience after a reduction in population size caused by disturbance events such as floods, we ran a set of simulations in which the effect of floods on population abundance was explicitly accounted for by means of the fuzzy function reported in Fig. 1 (VB-F and DD-F scenarios) and another set of simulations in which flood events were not included in the model (VB-NF and DD-NF scenarios).

For each of the four scenarios (VB-F, DD-F, VB-NF, DD-NF), the population dynamics of marble trout was thus simulated as follows:

(1)   In the case of DD-growth, mean length $\bar{L}_{1+}$ of a cohort was estimated with Eq. (4). The actual body length of each individual at age 1+ was then computed by randomly drawing a deviate from the log-normal distribution with mean $\log(\bar{L}_{1+})$ and standard deviation equal to 0.13—which is the mean of the standard deviations of the lognormal distributions fitted on cohort-specific L_{1+} data (Vincenzi et al. 2007b).

(1.1) In the case of VB-growth, for each marble trout the parameters L_∞, k and x_0 of the stream-specific Von Bertalanffy growth curves (Vincenzi et al. 2007b) were randomly drawn from the uniform distribution over their respective 95% confidence intervals (Table 1) and kept constant through marble trout lifetime. The uniform distribution was chosen to stress the uncertainty in parameters estimation.

(2)   In the case of DD-growth, annual individual growth rates of marble trout at subsequent ages were estimated by applying Eq. (5), with regression coefficients randomly drawn from the uniform distribution over their respective 95% confidence intervals (Table 1). The density of marble trout was computed by dividing the total number of adult marble trout by the overall pool surface in the stream, kept constant during the simulations.

(2.1) In the case of VB-growth, the length of each marble trout at age x was computed by using the Von Bertalanffy growth function (Eq. 3) with the growth parameters L_∞, k and x_0 previously drawn for each individual.

(3)   The expected annual survival rate of marble trout aged $\geq 1+$ σ_A for Zakojska and Gorska was randomly drawn at each time step from the uniform distribution over the 95% confidence interval (Table 1). As the maximum age for marble trout living in the study area is 6+, the survival rate of individuals aged 6+ was set to 0.

(4)   In the simulations in which flood events were explicitly included (DD-F and VB-F scenarios), the mortality induced by floods [$F(t)$] was estimated each year by first randomly drawing a rainfall value from the log-normal distribution of October rainfalls recorded from 1961 to 2004 and then by using the non-linear fuzzy function reported in Fig. 2 to compute the flood-induced mortality factor $F(t)$. Population size was then reduced in each age–class according to $F(t)$. In simulations in which floods were not included (DD-NF and VB-NF), the flood-induced mortality factor F was set to 0 for the whole simulation time (no flood-induced mortality).

(5)   The number of eggs produced by a female was estimated as a function of total length by using Eq. (1). The overall number of eggs produced each year was thus given by the sum of the number of eggs produced by each reproductive female in the population. The sex ratio of eggs was set at 1:1. Females were assumed to be sexually mature at age 3+ and 4+ if $L_T \geq 200$ mm, while only 20% of females aged 5+ were randomly assumed to spawn (rounded to the next unit).

Survival from eggs to 1+ was estimated by applying Eq. (2) with parameters a and γ randomly chosen each year from the uniform distribution over their respective confidence intervals (Table 1).

The two approaches (VB and DD) are thus identical except for the way in which they model individual growth. The individual-based model was run for the population of Gorska and for the population of Zakojska for 1000 replicates of 100 years each for each of the four scenarios. A period of 100 years is a reasonable time span as the generation time of marble trout living in the study area is 3.5 years (Crivelli, unpublished data).

For each replicate, the initial population was set to the number of marble trout translocated in both Zakojska and Gorska when creating the new population, namely 500 individuals aged 1+. Also in this case, we performed a sensitivity analysis by randomly drawing the initial number of individuals aged 1+ from a uniform distribution bounded between 300 and 700. For each replicate we computed a set of demographic indexes to evaluate population performances, namely: (1) the quasi-extinction risk, which is the probability that adult population abundance ($\sum_{i=1+}^{6+} n_I$, where n_I is the number of marble trout in each age class) drops below a given threshold in population abundance ranging between 0 and 100 individuals during the simulation time; (2) mean adult population abundance across the simulation time, considering only the replicates in which the population did not go extinct; (3) the mean of the per capita number of eggs produced by sexually mature females across the simulation time; (4) the mean age-specific length for marble trout across the simulation time. One-tailed paired randomization tests (Manly 1997) were used to test differences between demographic indexes in alternative scenarios in each stream (DD-F vs. VB-F and DD-NF vs. VB-NF) as follows: (1) a value θ_j of the demographic index to be tested was randomly selected from the distribution obtained by simulating the first scenario to be compared; (2) a second value θ_k ($k \neq j$) was randomly drawn from the distribution obtained by simulating the other scenario to be compared; (3) the difference between θ_j and θ_k was computed. The steps (1–3) were replicated 10,000, times and the significance level P was then computed as the fraction of times the difference between θ_j and θ_k was strictly negative (or positive). Significance level for the one-tailed randomization tests was set at 0.05.

Results

The mean population sizes estimated in the four scenarios (Fig. 3a) were similar to those observed during the study period in Zakojska (284.61 ± 72.27 marble trout) and Gorska (90.42 ± 34.04). Further simulations, not reported here, that were performed without density-dependence in first-year survival and by setting σ_0 equal to the mean of the first-year survival rates estimated from 1999 to 2004 provided unreasonably high abundances for both streams. This confirms the role of density-dependence in first-year survival in regulating the upper limit of population size.

When flood events were explicitly included in the simulations (VB-F and DD-F scenarios), the probability of quasi-extinction was substantially lower when individual growth was density-dependent (DD-F scenario) both in Zakojska and in Gorska (Fig. 4). In contrast, when flood events were not included in the simulations (VB-NF and DD-NF scenarios), the quasi-extinction risk was basically the same for both growth scenarios for both populations and was negligible for low quasi-extinction thresholds.

When growth was density-dependent, the mean individual body length of marble trout cohorts aged 1+ typically increased when the abundance of marble trout dropped after a major flood event (scenario DD-F; Fig. 5). This result of the simulation analysis is supported by the increase in mean length of marble trout after a flood event observed in Zakojska. A one-tailed t test on log-transformed mean length of marble trout aged 1+ sampled in Zakojska in June 2004 and June 2005 (before and after the October 2004 flood, respectively) showed a significant difference ($P < 0.05$), with marble trout sampled after the flood presenting a greater mean length (2004: $n = 77$, $L_T = 107.05 \pm 14.82$; 2005: $n = 64$, $L_T = 118.55 \pm 23.70$).

In both streams, mean population abundance when age-specific growth was density-dependent (DD-F scenario) was significantly higher than when growth was assumed to be density-independent (randomization test $P < 0.01$ in both streams; Fig. 3a). Similarly, the mean per-capita egg production and mean age-specific length were higher in the DD-F scenarios in both streams (randomization test $P < 0.01$).

When flood events were not included in the model, the randomization tests for both streams did not show any significant difference between the VB-NF and DD-NF scenarios in mean population abundance and mean per-capita egg production ($P > 0.05$ for all demographic indexes) (Fig. 3a, b). Significant differences in mean age-specific length between the VB-NF and DD-NF scenarios were found only for the Gorska population for marble trout aged 5+ and 6+ ($P < 0.05$) (Fig. 3c, d).

Simulations performed with values of F_{max} ranging from 0.6 to 0.8 and with an initial population size varying from 300 to 700 marble trout aged 1+ provided essentially the same results, indicating a low sensitivity of the individual-based model of population dynamics to variation of these parameters (see Electronic Supplementary Material).

Discussion

This study shows that density-dependent individual growth in marble trout populations allows a faster recovery after population collapses due to disturbance events, such as

Fig. 3 Histograms of demographic indexes computed from four simulation scenarios for Zakojska and Gorska marble trout populations. **a** Population abundance, **b** per-capita egg production, **c, d** age-specific individual length of marble trout for Zakojska (**c**) and Gorska (**d**). The following scenarios were simulated: *DD-NF* density-dependent individual growth with no occurrence of flood events, *VB-NF* Von Bertalanffy individual growth with no occurrence of flood events, *DD-F* density-dependent individual growth with occurrence of flood events, *VB-F* Von Bertalanffy individual growth with occurrence of flood events. All panels show mean ± SD

a Zakojska

b Gorska

Scenario VB-F

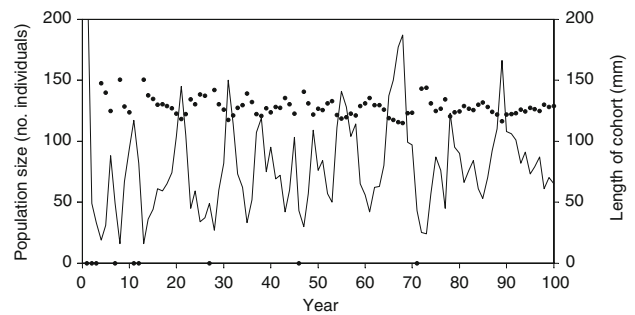Scenario DD-F

Scenario VB-NF

Scenario DD-NF
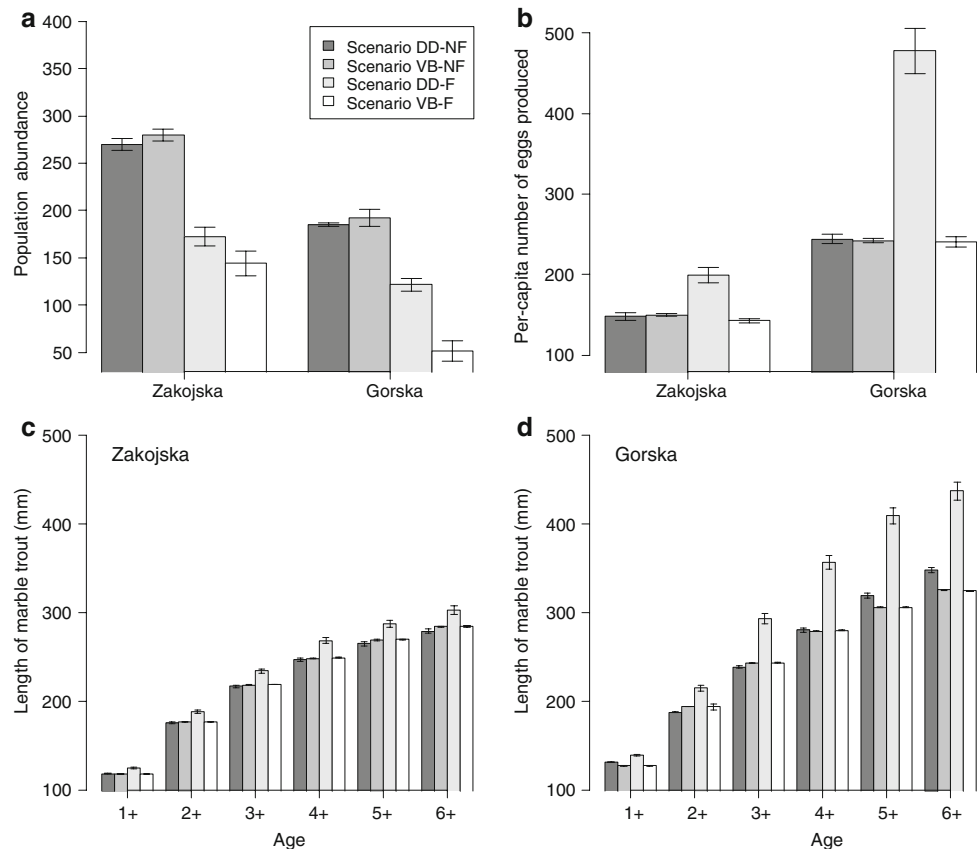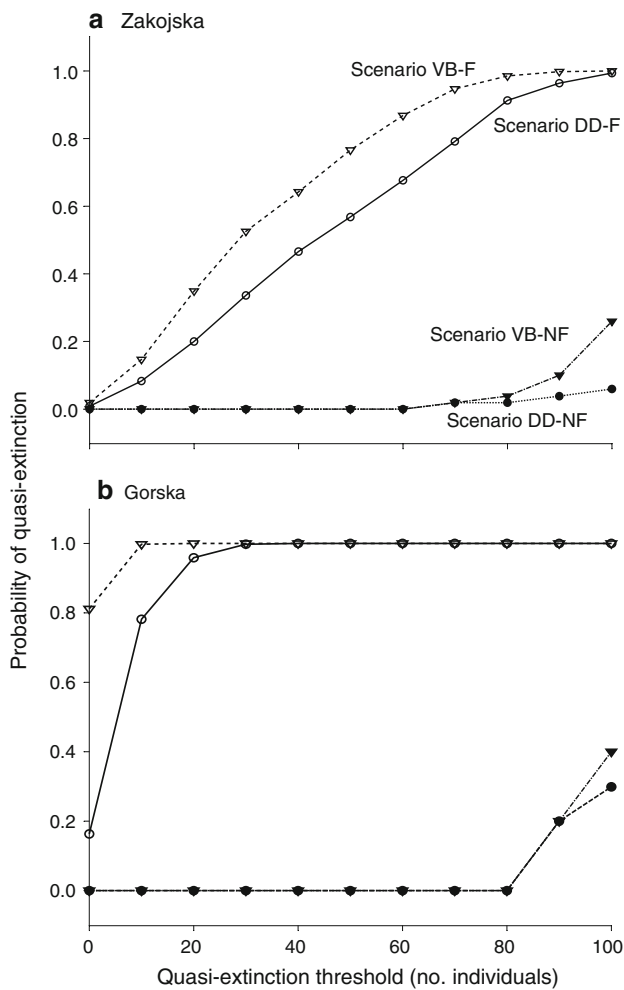
Fig. 4 Probability of quasi-extinction for four simulation scenarios with a quasi-extinction threshold ranging from 0 to 100 individuals for the marble trout populations of Zakojska (**a**) and Gorska (**b**). For definition of scenarios, see caption to Fig. 3

Fig. 5 Example of 100-year simulation replicate with density-dependent growth and the occurrence of flood events under the DD-F scenario for the Gorska marble trout population displaying variations in mean individual length of cohorts aged 1+ (*filled circle*) in response to variations in populations size ($\sum_{i=1+}^{6+} n_I$, where n_I is the number of marble trout in each age class, *solid line*). Mean lengths equal to 0 means that there were no marble trout aged 1+ present in that year

major floods, and thus lowers the risk of quasi-extinction. In simulations that factored in the occurrence of flood events, the risk of quasi-extinction was lower for both Gorska and Zakojska marble trout populations when individual growth was modelled using the empirical model of density-dependent growth (DD-F scenario) than when modelled with the VB-F scenario, in which individual growth followed the Von Bertalanffy growth curve; this was particularly evident for low quasi-extinction thresholds. In fact, in the case of density-dependent individual growth, exogenous events, such as severe floods, may trigger the following chain of direct and indirect impacts: first, severe floods remarkably reduce population abundance by flushing away or killing marble trout. Hence, provided that suitable habitat remains that is unaffected by the flood, individual growth of surviving juvenile and adult individuals increases due to a relaxing of density-dependent intra-specific competition (Fig. 5). As a consequence

of the increased growth rate, females are expected to be larger at sexual maturity and, given the positive relationship between female body length and fecundity, they are also expected to produce more eggs. The increased fertility allows the surviving population to recover faster than if there were no effects of density on individual growth, thus reducing the risk of quasi-extinction. In summary, in a variable environment, density-dependent growth ultimately increases the probability of persistence of marble trout populations (Fig. 4). The lower quasi-extinction risk exhibited in DD-F and VB-F scenarios by the marble trout population of Zakojska with respect to the Gorska population (Fig. 4) is a consequence of the lower mean population size of the latter (Fig. 3a), which increases the probability of falling below a given quasi-extinction threshold even in the case of moderate flood events. The lower mean population size of Gorska observed both in the wild and in the simulation results is related to the scarcity of suitable micro-habitat for juveniles, which affects first-year survival (lower for Gorska; Vincenzi et al. 2007a) and seems to be the predominant limiting factor to mean population size (Vincenzi et al. 2008).

In contrast, in scenarios where flood events were not included (VB-NF and DD-NF) for both marble trout populations, the risk of quasi-extinction (Fig. 4) and the values of the demographic indexes (Fig. 3) were basically the same in the two scenarios, regardless of the type of individual growth considered. Moreover, with low quasi-extinction thresholds, the risk of quasi-extinction for both VB-NF and DD-NF scenarios was negligible (Fig. 4). Therefore, the role of density-dependent individual growth in the persistence of marble trout populations appears to be particularly important in the case of a drastic reduction in population abundance, such as after the occurrence of a severe flood event. The resilience of marble trout

populations to flood events is also confirmed by empirical evidence, as the population size in a majority of the remnant populations living in the study area quickly rebounded to pre-event levels after the October 2004 flood (Fig.I1). In contrast, in streams with fairly stable hydrological conditions, density-dependent first-year survival plays a prominent role in regulating population abundance by acting as a demographic bottleneck at high population densities (Vincenzi et al. 2008). With respect to the differences observed between the Zakojska and Gorska populations in simulation results for both mean per-capita number of eggs produced (Fig. 3b) and mean length of individuals (Fig. 3c, d), the lower density of the marble trout of Gorska (Fig. 3a) allows greater individual growth rates due to the their density-dependence (Eqs. 4 and 5) and, consequently, greater per-capita egg productions—given the positive relationship between female length and fecundity—with respect to the Zakojska population. The pattern is also confirmed by the higher individual growth rates of marble trout living in Gorska, relative to the Zakojska population, that were observed in the study period (Vincenzi et al. 2007b). Moreover, the greater strength of the relationship between density and individual growth estimated for the Gorska population (Table 1) explains the remarkable greater mean per-capita number of eggs produced (Fig. 3b) and mean age-specific length of marble trout (Fig. 3d) observed in the DD-F scenario relative to the other three scenarios. Our results seem to suggest that both compensatory processes may be operating continuously and simultaneously in salmonid populations. However, their relative importance on population dynamics depends on population density, with density-dependent individual growth and its effects on fecundity having the more important role of quickly increasing population abundance at low densities.

Other salmonid species in freshwater habitats exhibit a considerable resilience to extreme flood events, with disturbed populations typically returning to pre-event densities within 3 years (Lamberti et al. 1991; Swanson 1998) unless the event created unsuitable habitat conditions. Jenkins et al. (1999) pointed out that high individual growth rates at low densities may enable the populations to rebound quickly after catastrophic density-independent mortality events, such as extreme floods caused by snowmelt peaks. Roghair et al. (2002) reported that a brook trout population living in the Staunton River (Virginia, USA) quickly recovered after a catastrophic debris-flow. Moreover, significant differences in brook trout length were found between sites affected or unaffected by the debris-flow: the average lengths of juveniles in the affected area were consistently greater than those in the unaffected area for the 2 years immediately following the flood. The same pattern was observed in Zakojska, where the mean individual length of marble trout aged 1+ was significantly greater the year after the flood event. In other studies, increased growth rates have been observed for juvenile and adult salmonids occupying disturbed areas (Elwood and Waters 1969; Lamberti et al. 1991; Letcher and Terrick 1998); this increased growth was generally attributed to an increased food supply and/or decreased competition due to a low population density following the event. Similarly, in Zakojska, increased individual growth of marble trout was observed after the October 2004 flood. As pointed out by Roghair et al. (2002), an increase in juvenile growth, such as that observed immediately following a flood event that reduces population density, can decrease age-at-maturity due to faster growth rates and/or increase fecundity (Hutchings 1996) and suggests a mechanism that has developed to allow populations to quickly increase their numbers when decimated by events such as debris flows or severe floods. Another example of the resilience of salmonid populations is represented by the Gila trout population of McKnight Creek in the Gila River Drainage (New Mexico and Arizona, USA), which recovered within a few years to pre-event conditions after a catastrophic flood that caused a 90% drop in population abundance (Propst and Stefferud 1997).

Our individual-based model is based on information available on the population dynamics of marble trout living in Slovenian streams, but additional research is needed to improve our understanding of the value of density-dependent individual growth in terms of population regulation and persistence. For example, the modelling of flood events and of the consequent reduction in population abundance for marble trout populations living in the study area may be substantially improved when more detailed meteorological and hydrological information becomes available. Moreover, severe flood events can greatly perturb suitable habitats for freshwater fishes through altering the spawning grounds and/or stream morphology, an aspect not included in the current version of the model. Future studies will be aimed at assessing whether density-dependent growth, especially during the first year of life, could translate into density-dependent survival over the first winter, as argued by Post et al. (1999). Another proposed mechanism by which density-dependent growth may contribute to the numerical regulation of stream-living salmonids is that larger females may produce bigger eggs, resulting in increased survival of more abundant and larger juveniles (e.g. Hendry and Day 2003). The potential for cannibalism and its effects on population dynamics also deserve future investigation, as it is generally recognized that cannibalism may have two main population-level effects: stabilization of population numbers (Dong and Polis 1992) and alteration of size distribution (Crowley and Hopper 1994). Moreover, especially in fragmented

streams, the movement of fish, both density-dependent and density-independent, and its relationship with population dynamics are worthy of investigation. It is well known that competition for feeding and spawning sites in many stream-dwelling salmonid populations involves the fine-scale movement of individuals related to body size (Caron and Beaugrand 1988; Grant et al. 1998; Hughes 1998) and can thus influence population dynamics. Thus, a spatially-explicit individual-based model of population dynamics may provide other insights on the role of density-dependent growth in population dynamics. However, it is worth noting that while even decades of data may not be sufficient to reduce the uncertainty in crucial model parameters (Ludwig 1999), the results of the simulation analyses are still valuable when interpreted relative to other scenarios (Lindenmayer and Possingham 1996), as it has been done in our study.

In conclusion, we believe that the results of the analysis presented here strongly indicate that density-dependent individual growth has a potentially powerful role in the population regulation of stream-dwelling salmonids by enhancing the resilience of salmonid populations to catastrophic disturbances.

References

Achord S, Levin PS, Zabel RW (2003) Density-dependent mortality in Pacific Salmon: the ghost of impacts past? Ecol Lett 6:335–342

Berrebi P, Povz M, Jesensek D, Crivelli AJ (2000) The genetic diversity of native, stocked and hybrid populations of Marble trout in the Soca River, Slovenia. Heredity 85:277–287

Caron J, Beaugrand JP (1988) Social and spatial structure in brook chars (*Salvelinus fontinalis*) under competition for food and shelter/shade. Behav Process 16:173–191

Cattaneo F, Lamouroux N, Breil P, Capra H (2002) The influence of hydrological and biotic processes on brown trout (*Salmo trutta*) population dynamics. Can J Fish Aquat Sci 59:12–22

Coulson T, Mace GM, Hudson E, Possingham H (2001) The use and abuse of population viability analysis. Trends Ecol Evol 16:219–221

Craig JF, Kipling C (1983) Reproductive effort versus the environment; case histories of Windemere perch, *Perca fluviatilis* L. and pike, *Esox lucius* L. J Fish Biol 22:713–727

Crivelli A, Poizat G, Berrebi P, Jesensek D, Rubin JF (2000) Conservation biology applied to fish: the example of a project for rehabilitating the marble trout (*Salmo marmoratus*) in Slovenia. Cybium 24:211–230

Crowley PH, Hopper KR (1994) How to behave around cannibals: a density-dependent dynamic game. Am Nat 143:117–154

Dong Q, Polis GA (1992) The dynamics of cannibalistic populations: a foraging perspective. In: Elgar MA, Crespi BJ (eds)

Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, New York, pp 13–37

Einum S (2005) Salmonid population dynamics: stability under weak density dependence? Oikos 110:630–633

Elliott JA (1994) Quantitative ecology and the brown trout. Oxford University press, Oxford

Elliott JM (1993) The pattern of natural mortality throughout the life-cycle in contrasting populations of brown trout, *Salmo Trutta* L. Fish Res 17:123–136

Elliott JM, Hurley MA, Elliott JA (1997) Variable effects of droughts on the density of a sea-trout *Salmo trutta* population over 30 years. J Appl Ecol 34:1229–1238

Elwood JW, Waters TF (1969) Effects of floods on food consumption and production rates of a stream brook trout population. Trans Am Fish Soc 98:253–262

Forneris G, Del Mastro GB, Bellardi S (1990) Attuale distribuzione di *Salmo marmoratus* Cuvier, 1817 in Provincia di Torino. Riv Idrobiol 29:213–221

Fumagalli L, Snoj A, Jesensek D, Balloux F, Jug T, Duron O, Brossier F, Crivelli AJ, Berrebi P (2002) Extreme genetic differentiation among the remnant populations of marble trout (*Salmo marmoratus*) in Slovenia. Mol Ecol 11:2711–2716

Grant JWA, Imre I (2005) Patterns of density dependent growth in juvenile stream-dwelling salmonids. J Fish Biol 67:100–110

Grant JWA, Steingrimsson SO, Keeley ER, Cunjak RA (1998) Implications of territory size for the measurement and prediction of salmonid abundance in streams. Can J Fish Aquat Sci 55:181–190

Grossman GD, Moyle PB, Whitaker JO (1982) Stochasticity in structural and functional-characteristics of an Indiana stream fish assemblage—a test of community theory. Am Nat 120:423–454

Grossman GD, Ratajczak RE, Crawford M, Freeman MC (1998) Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. Ecol Monogr 68:395–420

Hansen LP, Jonsson B, Morgan RIG, Thorpe JE (1989) Influence of parr maturity on emigration of smolting Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 46:410–415

Harrell HL (1978) Response of the Devil's River fish community to flooding. Copeia 1978:60–68

Hendry AP, Day T (2003) Revisiting the positive correlation between female size and egg size. Evol Ecol Res 5:421–429

Hixon MA (1980) Food production and competitor density as the determinants of feeding territory size. Am Nat 115:510–530

Hixon MA, Pacala SW, Sandin SA (2002) Population regulation: historical context and contemporary challenges of open vs. closed systems. Ecology 83:1490–1508

Hughes NF (1998) A model of habitat selection by drift-feeding stream salmonids at different scales. Ecology 79:281–294

Hutchings JA (1996) Adaptive phenotypic plasticity in brook trout, *Salvelinus fontinalis*, life histories. Ecoscience 3:25–32

Hutchings JA, Jones MEB (1998) Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Can J Fish Aquat Sci 55:22–47

Jenkins TM, Diehl S, Kratz KW, Cooper SD (1999) Effects of population density on individual growth of brown trout in streams. Ecology 80:941–956

Jensen AJ, Johnsen BO (1999) The functional relationship between peak spring floods and survival and growth of juvenile Atlantic Salmon (*Salmo salar*) and Brown Trout (*Salmo trutta*). Funct Ecol 13:778–785

Keddy PA (1989) Competition. Chapman and Hall, London

Klemetsen A et al (2003) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecol Freshw Fish 12:1–59

Koops MA, Hutchings JA, McIntyre TM (2004) Testing hypotheses about fecundity, body size and maternal condition in fishes. Fish Fish 5:120–130

Koslow JA (1992) Fecundity and the stock-recruitment relationship. Can J Fish Aquat Sci 49:210–217

Lake PS (2000) Disturbance, patchiness, and diversity in streams. J North Am Benthol Soc 19:573–592

Lamberti GA, Gregory SV, Ashkenas LR, Wildman RC, Moore KMS (1991) Stream ecosystem recovery following a catastrophic debris flow. Can J Fish Aquat Sci 48:196–208

Lennon RE (1961) The trout fishery in Shenandoah National Park. Special Scientific Report Fisheries 395, U.S. Fish and Wildlife Service, Washington D.C.

Letcher BH, Terrick TD (1998) Maturation of male age-0 Atlantic salmon following a massive, localized flood. J Fish Biol 53:1243–1252

Lindenmayer DB, Possingham HP (1996) Ranking conservation and timber management options for leadbeater's possum in southeastern Australia using population viability analysis. Conserv Biol 10:235–251

Lobon-Cervia J (1996) Response of a stream fish assemblage to a severe spate in Northern Spain. Trans Am Fish Soc 125:913–919

Lobon-Cervia J, Rincon PA (2004) Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout Salmo trutta. Oikos 105:641–646

Lorenzen K, Enberg K (2002) Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proc R Soc Lond Ser B Biol Sci 269:49–54

Ludwig D (1999) Is it meaningful to estimate a probability of extinction? Ecology 80:298–310

Manly FJ (1997) Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall, London

McCullagh P, Nelder JA (1989) Generalized linear models. CRC Press, Boca Raton

Meldgaard T, Crivelli AJ, 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. Biol Conserv 136:602–611

Milner NJ, Elliott JM, Armstrong JD, Gardiner R, Welton JS, Ladle M (2003) The natural control of salmon and trout populations in streams. Fish Res 62:111–125

Morris FM, Doak DF (2002) Quantitative conservation biology. Sinauer Assoc, Sunderland

Nikolsky J (1969) Theory of fish population dynamics as the background for rational exploitation and management of fishery resources. Oliver and Boyd, Edinburgh

Nikolsky J, Bogdanov A, Lapin Y (1973) On fecundity as a regulatory mechanism in fish population dynamics. Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mer 164:174–177

Post JR, Parkinson EA, Johnston NT (1999) Density-dependent processes in structured fish populations: interaction strengths in whole-lake experiments. Ecol Monogr 69:155–175

Povz M, Jesensek D, Berrebi P, Crivelli AJ (1996) The Marble trout, Salmo trutta marmoratus, Cuvier 1817, in the Soca River basin, Slovenia. Tour du Valat Publication, Arles

Propst DL, Stefferud JA (1997) Population dynamics of Gila trout in the Gila River drainage of the south-western United States. J Fish Biol 51:1137–1154

Roghair CN, Dolloff CA, Underwood MK (2002) Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. Trans Am Fish Soc 131:718–730

Rose KA, Cowan JH, Winemiller KO, Myers RA, Hilborn R (2001) Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish Fish 2:293–327

Rothschild BJ, Fogarty MJ (1989) Spawning-stock biomass: a source of error in recruitment/stock relationships and management advice. J Conseil International pour l'Exploration de la Mer 45:131–135

Schoffmann J (1994) Zur gegenwätigen Situation des marmorierten Forelle (Salmo marmoratus Cuvier, 1817) in Albanien, ihrem südlichsten Verbreitungsraum. Osterreichs Fischerei 47:132–136

Seegrist DW, Gard R (1972) Effects of floods on trout in Sagehen Creek, California. Trans Am Fish Soc 101:478–482

Sommani E (1961) Il Salmo marmoratus Cuv.: sua origine e distribuzione nell'Italia settentrionale Bollettino di Pesca. Piscicolt Idrobiol 15:40–47

Sousa WP (1984) The role of disturbance in natural communities. Annu Rev Ecol Syst 15:353–391

Swanson BJ (1998) Autocorrelated rates of change in animal populations and their relationship to precipitation. Conserv Biol 12:801–808

Utrilla CG, Lobon-Cervia J (1999) Life-history patterns in a southern population of Atlantic salmon. J Fish Biol 55:68–83

Vincenzi S, Crivelli AJ, Jesensek D, Rubin JF, De Leo GA (2007a) Early survival of marble trout Salmo marmoratus: evidence for density dependence? Ecol Freshw Fish 16:116–123

Vincenzi S, Crivelli AJ, Jesensek D, Rubin JF, De Leo GA (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 AJ, Jesensek D, Rubin JF, Poizat G, De Leo GA (2008) Potential factors controlling the population viability of newly introduced endangered marble trout populations. Biol Conserv 141:198–210

Weng ZY, Mookerji N, Mazumder A (2001) Nutrient-dependent recovery of Atlantic salmon streams from a catastrophic flood. Can J Fish Aquat Sci 58:1672–1682