Rev Fish Biol Fisheries (2012) 22:437–455
DOI 10.1007/s11160-011-9235-5

RESEARCH PAPER

Translocation of stream-dwelling salmonids in headwaters: insights from a 15-year reintroduction experience

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Received: 22 March 2011 / Accepted: 18 August 2011 / Published online: 15 September 2011

Abstract Translocation programs are a common strategy to increase the number of viable populations of threatened freshwater fishes. Yet, only in a minority of cases the success or failure of translocations has been assessed through a quantitative analysis of demographic traits, compensatory responses, life-histories and population dynamics of the threatened species. A paradigmatic case a translocation program combining both management- and research-oriented activities is represented by the Marble Trout Conservation Program, which started in 1993 in the upper reaches of the Soca, Idirjca and Baca river basins (Slovenia) for the conservation of stream-dwelling marble trout *Salmo marmoratus*. In order to enhance the viability of the species, two new populations were created in 1996 by stocking 500 marble trout aged 1+ in previously fishless streams (Gorska and Zakojska) within the core habitat of the species. The new populations have been systematically monitored for 15 years by individually tagging and sampling marble trout. Our analyses show that deterministic extinction of marble trout populations are unlikely and that high-magnitude environmental stochasticity (i.e., severe floods) is the only main cause of local population extinction, despite the high resilience to flood-induced massive mortalities exhibited by marble trout through compensatory mechanisms (e.g., relaxation of density-dependent body growth and survival at low densities). Fishless headwaters, probably characterized by a history of recurrent severe floods, should not be considered as candidate sites for the creation of new populations. Fewer individuals than originally reintroduced (i.e., 500 fish aged 1+ in each stream) might be sufficient to establish viable populations, since compensatory mechanisms are likely to regulate population size around stream carrying capacity in a few years. Besides enhancing the species viability, translocation programs can provide an excellent framework for the estimation of ecological traits (e.g., life-histories, demography, population dynamics

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etc.), identify potential vulnerabilities and thus guide well-formed management actions for the threatened species.

Keywords Translocation · Reintroduction · Marble trout · Flood · Establishment · Persistence

Introduction

About one-third of the known European freshwater fish species are endangered or are facing the risk of extinction (Kottelat and Freyhof 2007). The main causes of the decline are all anthropic: habitat destruction and fragmentation, water quality deterioration, overexploitation and the introduction of alien species (Cowx and Collares-Pereira 2002). All these factors have contributed to genetic and ecological alterations leading to a decline of population abundance, a contraction in the area of distribution and, as a final result, to the local extinction of an impressive number of freshwater fish species. Presently, 56% of the 252 endemic freshwater Mediterranean fish are threatened with extinction (Smith and Darwall 2006).

At least 80% of recovery programs for fish–mainly carried out in the US–suggest translocations as an effective means to enhance the viability of the threatened species (Williams et al. 1988). We use translocation as general term defining any movement of living organisms from one area to another, including introduction (movement of an organism outside its historically known native range), reintroduction (movement of an organism into a part of its native range from) and restocking of fish (movement of individuals to build-up an existing population) (Armstrong and Seddon 2008). The success rate of translocation programs for birds, mammals and fish is generally low (<50%, Williams et al. 1988; Fischer and Lindenmayer 2000; Armstrong and Seddon 2008) and published literature on translocations is biased towards positive results (Deredec and Courchamp 2007). In most cases, the causes of the low success rate of translocation programs remain basically unknown, since the majority of translocation projects was either not supported by a systematic monitoring of translocated populations or implemented only sparse monitoring schemes, with sampling surveys occurring every 3–5 years (see Maitland et al. 2007 for paradigmatic cases relative to Artic Charr *Salvelinus alpinus* in Britain and Ireland, Armstrong and Seddon 2008). The immediate aim of a translocation is to relocate sufficient individuals to establish a new population successfully, but although population establishment is essential for successful translocations, recovery programs should also aim to maximize the chances of long-term persistence of new populations.

Nearly all salmonid species have endemic populations that recently went extinct or became endangered (Williams et al. 1989; Behnke 1992) and massive efforts are ongoing to identifying and restoring suitable habitat for salmonids (e.g., Armstrong et al. 2003). Among trout species, marble trout *Salmo marmoratus* (Cuvier) (Kottelat 1997) is of particular conservation interest, since only few pure populations remain viable today in a restricted geographical distribution in the basin of Po in northern Italy (e.g., Sommani 1961), in the Adriatic basin of former Yugoslavia (Povz 1995) and Albania (Schoffmann 1994, but see Snoj et al. 2009).

The Marble Trout Conservation Program (MTCP) started in 1993 in the upper reaches of the Soca, Idrijca and Baca river basins in Slovenia (Fig. 1). Seven genetically pure marble trout populations (less than 2% of foreign genes, Berrebi et al. 2000) were discovered in remote headwater streams (Fig. 1, before MTCP only the population of Zadlascica was known, Povz 1995), where waterfalls prevent the upstream movement of brown, hybrid brown/marble and rainbow trout (Crivelli et al. 2000; Vincenzi et al. 2011a), and thus gene introgression or displacement of native populations. Besides the conservation and protection of the remnant populations, the MTCP goals included the duplication of the existing populations through reintroductions of marble trout in suitable fishless and pristine (i.e., no anthropogenic disturbance) streams into its native range to enhance the long-term viability of the species (Crivelli et al. 2000).

MTCP attempted to overcome the most common limitations of translocation programs. The long-term monitoring scheme which followed the creation of Gorska and Zakojska marble populations (Fig. 1) was set up to both reach management objectives and to deal with the key questions of reintroduction biology at the population level, that is to identify factors affecting the establishment and the

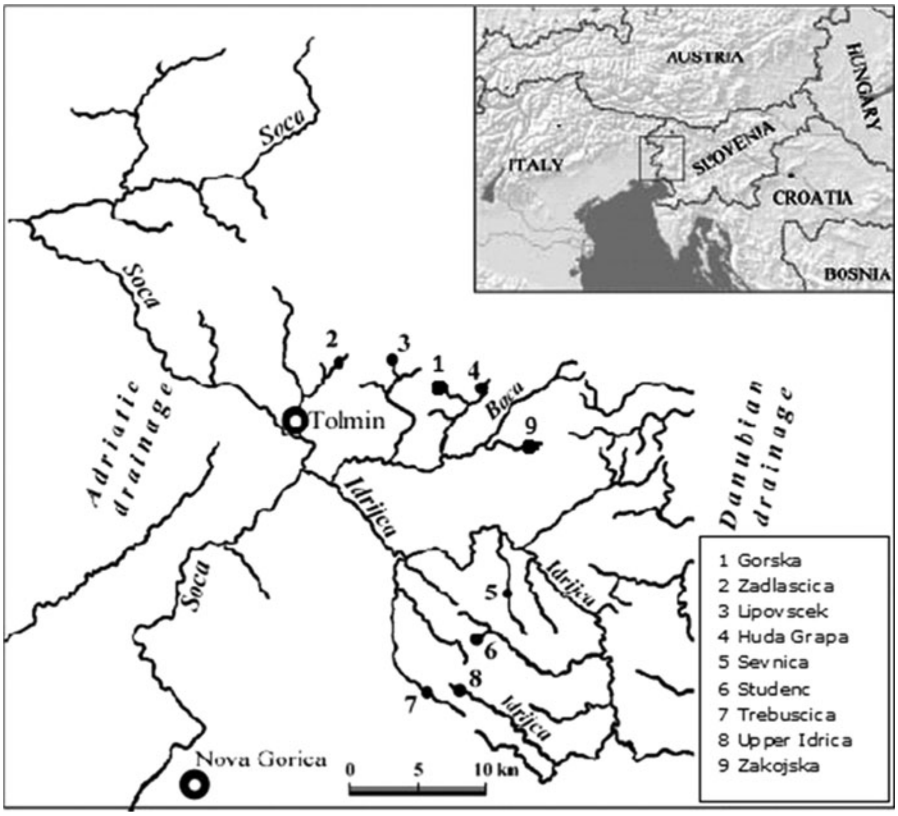

Fig. 1 Location of *S. marmoratus* populations within the Soca, Idrijca and Baca river basins in in northwestern Slovenia. Marble trout were reintroduced in Gorska and Zakojska

persistence of reintroduced populations (Armstrong and Seddon 2008). Specifically, for the establishment of populations, the two key questions that we intended to address with MTCP were: (1) "how is establishment probability of populations affected by the size and composition of the release group?", and (2) "how are post-release survival and dispersal of reintroduced fish affected by pre- and post-release management?" (Armstrong and Seddon 2008). Composition and management of release groups should aim to avoid both a rapid extinction due to demographic events and the selection of life-histories adaptive in captivity, but maladaptive in natural conditions (e.g., selection of better competitors at the higher population densities experienced in the fish farm). As for population persistence after the successful establishment, the key question that we intended to address with MTCP was: "what habitat conditions are needed for persistence of the reintroduced population?" (Armstrong and Seddon 2008). Here, habitat conditions and quality should be intended as the general features of the environment that are appropriate for individual and population persistence (e.g., water flow and quality, temperature, presence of water pools, etc.) (e.g., Harig and Fausch 2002). Success requires habitat of sufficient quality to meet the life-history requirements of the species (e.g., gravel to build spawning redds), of sufficient area to support a self-sustaining population despite demographic and environmental stochasticity, and of refuges from harsh events (e.g., snowmelt runoff or severe floods) or adverse environmental conditions (e.g., low or high temperatures).

While a number of technical papers have been published in recent years on statistical and demographic analysis of marble trout life-histories and population dynamics in Slovenia (Vincenzi et al. 2007a, b, 2008a, b), here we want to provide a comprehensive and synoptic view of the most relevant insights derived from MTCP. In particular, we intend to illustrate how the estimation of demographic and life-history traits, and responses to flood events—all integrated into models of population dynamics—allowed us to identify the factors determining the successful establishment and the persistence of the reintroduced populations, to predict their fate and to gather insights for the management of the seven remnant populations.

So far, the genetic aspects of translocation have been superficially approached (Vincenzi et al. 2010a) and are not discussed here, but they will be a relevant field for future investigations.

Materials and methods

Study area and species description

Marble trout is a stream-dwelling salmonid endemic to the Adriatic basin of Italy and former Yugoslavia, currently restricted to secluded headwater streams in northern Italy, Slovenia and Albania (Crivelli et al. 2000) (Fig. 1). In Slovenia, since the beginning of the last century (the first documented case dates back to 1906, Povz et al. 1996), brown trout *Salmo trutta* L. of different origins were introduced into the geographical area where marble trout is endemic, quickly leading to the creation of hybrid populations (Berrebi et al. 2000) and the loss of marble trout genetic integrity. Rainbow trout *Oncorhynchus mykiss* were introduced in the early twentieth century in Slovenian streams, one of the few places in Europe where rainbow trout established self–sustaining populations (probably due to a favorable pattern of disturbance events, Vincenzi et al. 2011a), and in some cases they successfully displaced native marble trout (Vincenzi et al. 2011a).

The Soca, Idirijca and Baca river basins present a relatively pristine environment with limited agricultural and industrial activities, absence of erosion due to deciduous forests, mainly *Fagus sylvatica*, low human population density and numerous officially protected areas, such as the Triglav National Park.

Marble trout inhabit streams with temperature between 2°C and 15°C. Marble trout is a most attractive angling trophy, but angling is allowed under a strict set of regulations only in the lower reaches of the Soca, Idrijca and Baca river basins, where populations are artificially restocked. Marble trout is better adapted to the harsh and variable conditions of headwater streams than alien salmonids (i.e., rainbow and brown trout) and thus offer there a fairly high biotic resistance to invasion (Meldgaard et al. 2007; Vincenzi et al. 2011a). *Salmo marmoratus* is phenotipycally and ecologically distinct from Mediterranean brown trout *S. trutta* and the *marmoratus* lineage is one of the five composing the *S. trutta* complex (Atlantic, Danubian, *marmoratus*, Mediterranean and Adriatic) (Bernatchez 2001). Detailed description of the biology and ecology of marble trout can be found in Crivelli et al. (2000), Delling (2000) and Vincenzi et al. (2007a, b, 2008a, b, 2010a, b, 2011a).

Marble trout show a high plasticity in body size; hybrid marble trout weighing up to 25 kg have been found in the lower reaches of the Soca river (Fumagalli et al. 2002) while in the headwater streams the maximum recorded weight was 650 g. In the study area, maximum recorded age for marble trout was 10 years, but very few individuals were older than 6 years. Marble trout feed generally on bottom-dwelling organism. Cannibalism by adult marble trout on juveniles is observed, although the extent of cannibalism and conditions leading to it are still not clear and deserve further investigations. Spawning takes place in November–December, eggs hatch generally in March, with emergence occurring in May–June. Data and direct observation show evidence of iteroparity (Meldgaard et al. 2007).

Reintroductions

In June 1996, 500 marble trout reared in the fish farm since birth were released as 1+ trout (stocking cohorts) in fishless headwaters of Zakojska and Gorska (Fig. 1). Trout were the progeny of mature marble trout females and males from the Zadlascica pure population (Fig. 1) caught in the wild in 1994; females were stripped in the fish farm and eggs reared up to fish aged 1+ within the fish farm (Tolminka, Tolmin, Slovenia). More details can be found in Crivelli et al. (2000). Fishing is not allowed in Gorska and Zakojska, and poaching was never observed due to the remoteness of the streams. The habitat features of Zakojska and Gorska are presented in Table 1. Gorska and Zakojska are both one-way streams, that is, marble trout can move only from upstream to downstream due to natural barriers (Vincenzi et al. 2008a) and no fish is present at higher altitudes. The stream bed of Gorska consists mainly of bedrock slides and is narrower than that of Zakojska and its flood plain is almost absent, with few shelter areas. On the contrary, in Zakojska, in case of flood the stream can overflow its bank on a wide area with riparian forest creating new suitable habitat for marble trout. Rainfall data has been acquired since 1961 (ARSO, Environmental Agency

Table 1 Main features of Gorska and Zakojska and of stocking cohorts used for the creation of marble trout populations

Main features	Zakojska	Gorska
Surface area of the catchment (km^2)	7.79	3.61
Land average slope of the catchment (%)	60.7	64.4
Length (m)	1238	845
Surface area (m^2)	3544	1805
Surface stream average slope (%)	22.5	22.8
Pool surface (m^2) (% of total surface)	895 (25.3%)	685 (38%)
Altitude range (m a.s.l.)	578–728	400–514
Benthos biomass (mg m^{-2})	14638	11446
Stocking date	June 1996	June 1996
Total number of reintroduced fish	500	500
Mean total length of reintroduced fish (mm) ± s.d.	115.15 ± 14.67	125.81 ± 15.54
Mean weight of reintroduced fish (g) ± s.d.	16 ± 8	22 ± 10
Mean body condition of reintroduced fish (K) ± s.d.	1.01 ± 0.12	1.06 ± 0.12

of Slovenia). The annual mean precipitation in the study area (Fig. 1) since 1961 was 2,400 mm, with October and November being the rainiest months.

Monitoring of populations

After the reintroduction, stocked trout successfully reproduced within the streams. We sampled marble trout hatched in the streams—along with stocking cohorts—every June since 1996 on the whole length of each stream starting from downstream to the upstream extent. We electrofished every stream two times to produce a multiple-pass removal estimate of trout abundance using Microfish 3.0 (Van Deventer and Platts 1989). All captured fish aged ≥1+ and with a minimum size of 115 mm (L_T) were anaesthetized with benzocaine, marked with Carlin tags (Institute of Freshwater Research, Sweden), measured for total length (L_T, to the nearest mm) and weight (W, g) and if sampled for the first time the adipose fin was removed. Marble trout then were returned live near the point of capture. Age was determined by tag examination. Age designation follows standard terminology; marble trout in the first year of life were denoted as 0+ and in the second year, subsequent to winter annulus formation, as 1+. At first marking, scales were taken to assess the age of the fish. The small size of marble trout aged 0+ prevents their sampling in June and they were thus excluded from the analyses. No sexing of trout caught could take place in June, since gonads development starts in late summer.

Analysis of flood events

In many salmonid populations, floods play an important role in the regulation of population dynamics (e.g., Jensen and Johnsen 1999) to the extent that in high-gradient streams, fish population dynamics and life-histories may be largely 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 and therefore a collapse of population size. In extreme cases, they can wash out the entire population and/or completely destroy fish habitat.

The dramatic impact of severe flood events on remnant and newly created marble trout populations became evident in October 2004, when flash-floods and debris-flows caused a reduction in population size ranging from 31 to 78%, from which the populations quickly recovered (Table 2; Fig. 2). The only exception was the population of Gorska, which was almost completely wiped out by a debris-flow. The catastrophic disturbance event had a presumable recurrence interval of 50–100 years, according to expert knowledge and to historical flow data (Slovenian Institute for water). Flash-floods in September 2007 caused a drastic reduction in population size in several populations, with the population of Zakojska–along with the remnant population of Lipovesck–reduced to a few individuals and still facing the risk of extinction (Fig. 2).

Most of the Slovenian streams where marble trout live are spring-fed. The intensity and frequency of floods vary greatly from year-to-year and among river basins, depending on spatial and temporal patterns of rainfall. The available information on the occurrence and intensity of floods (Table 2) and the analysis of their effects on the reintroduced and remnant marble trout populations living in the study area suggest an important role of moderate and severe flood events in

Table 2 Occurrence of flood events from 1999 to 2010 in streams where either remnant or reintroduced marble trout populations live

	Year											
Stream	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**
Remnant												
Huda			░			▓					░	
Lipovesck	▓	░			░	▓			▓		▓	░
Zadlascica	░					▓			▓		░	░
Trebuscica		░	░			▓	░				░	░
Studenc		░	░			▓	░				░	░
Upper Idrijca						░	░				░	░
Sevnica			░			▓	░				░	░
Reintroduced												
Zakojska						░			▓		░	
Gorska	░					▓						

Light gray moderate flood (recurrence interval = 10 to 20 years); *Dark gray* severe flood (r.i. = 50 to 100 years)

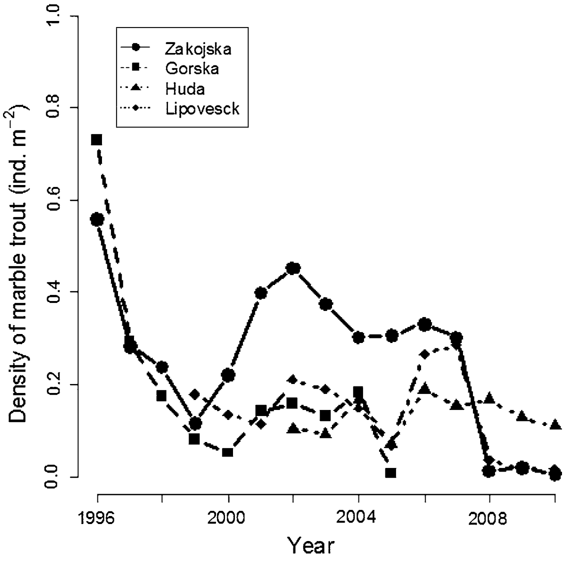

Fig. 2 Population density in Gorska and Zakojska (reintroduced populations) from 1996 to 2010 and in Lipovesck and Huda (remnant populations) from 1999 and 2002 to 2010, respectively. In October 2004 the marble population of Gorska went extinct due to a debris-flow and in September 2007 the population of Zakojska was almost totally wiped out by a flood. We used pool surface to estimate fish density

population dynamics of marble trout (Fig. 2). Therefore, flood events have been carefully accounted for in our models of population dynamics, as described hereafter.

Estimation of life-history traits

Here, we report a synthesis of the most salient elements and methods of the demographic and statistical analyses already published in a number of technical papers by the same authors of this work. We refer to them throughout the text for technical details.

Fecundity

33 wild females aged between 3 and 5 years old from the Zadlacisca pure population were stripped in the fish farm (Tolminka, Tolmin, Slovenia) to estimate fecundity. Females were returned to Zadlacisca after stripping. We estimated the relationship between body size of females and number of eggs produced using regression analysis. An assessment of successful spawning of pure marble trout living in the study area was performed using paternity investigation (Meldgaard et al. 2007).

Survival probabilities

We constructed a capture history representing the fate of an individual over the study period for each tagged marble trout. As only trout aged 1+ or older were tagged, we generated capture histories for a fish only if it was sampled at age ≥1+. Capture history matrices were used as input files the software MARK (White and Burnham 1999). Model selection was based on the Akaike Information Criterion (AIC; Lebreton et al. 1992; Burnham and Anderson 1998). Survival estimates were corrected by the tag-loss probability estimated in the corresponding stream. We tested for size-dependent survival at age 1+ $\cdots$ 4+ (we did not have enough data for 5+ individuals) using a generalized linear model (GLM, McCullagh and Nelder 1989). Details of the analyses can be found in Vincenzi et al. (2008a, b).

Compensatory responses to changes in population density

Density-dependent first-year survival

In order to investigate density-dependent survival of newly emerged marble trout, we combined a classical life table analysis with simulations following a MonteCarlo approach, as described in detail in Vincenzi et al. (2007a).

Density-dependent growth

Given the tight relationship between fecundity and body size in fish, density-dependent individual growth is a potentially powerful mechanism of population regulation (Jenkins et al. 1999; Lorenzen and Enberg 2002; Vincenzi et al. 2010b). Very little was known on the individual growth dynamics of marble trout before MTCP. We used regression analysis to test for the occurrence of density-dependent body growth in marble trout.

Population viability analysis (PVA)

PVA is the use of quantitative methods to predict the future status of a population, explicitly accounting for the effect of environmental variability and uncertainty in parameter estimation (Brook et al. 2000). Despite its predictive power and conceptual simplicity, only a minority (14%) of the recovery plans approved between 1991 and 2002 were supported by an extensive PVA (Morris and Doak 2002). In the context of MTCP, we used PVA to unveil the demographic mechanisms producing the observed population dynamics in Gorska and Zakojska and to support the creation of new populations through reintroductions.

We used two different modelling approaches. To assess the mean population performances and quasi-extinction probability (i.e., probability of dropping below a given threshold of population size), we developed an age-structured model of population dynamics (density-dependent Leslie matrix model, Caswell 2001), including also the occurrence of flood events. Then, we performed a sensitivity analysis of the matrix model in order to estimate the relative importance of vital rates and frequency and intensity of flood events on mean population size and the risk of quasi-extinction.

However, fish population dynamics can be better described when they emerge from lower level (i.e., individual fish) dynamics, especially when compensatory responses are identified and estimated. For instance, density-dependent body growth may lead to within- and among-cohorts differences in age at sexual maturity and per-capita number of eggs produced, with potential transgenerational effects and important consequences for population dynamics. Therefore, in order to overcome the inherent limitations of matrix models, we developed and applied an individual-based model (IBM). We used the IBM to analyze the role of compensatory responses (i.e., density-dependent body growth and first-year survival) for the persistence of marble trout populations. Both the matrix and the individual-based model did not include movement of trout and the populations were assumed to be closed. The two modelling approaches are briefly described hereafter.

Matrix model of population dynamics

In Fig. 3, we show the life-cycle diagram of marble trout living in the study area. Eggs are produced in autumn of year t and hatch in the spring of year $t + 1$, with juvenile marble trout reaching the age of 1+ in the spring of year $t + 2$. The model includes 7 age-classes, the first one accounting for the number of eggs and the other six for marble trout aged 1+, 2+ $\cdots$ 6+.

As for floods, we chose to model two uncorrelated type of events: one–severe flood–with a recurrence interval ranging from 50 to 100 years (T_1) and causing a random reduction in population size between 60 and 90% (r_1): the other event–moderate flood–with a recurrence interval ranging from 10 to 20 years (T_2) and causing a reduction in population size randomly between 10 and 40% (r_2). Once model parameters had

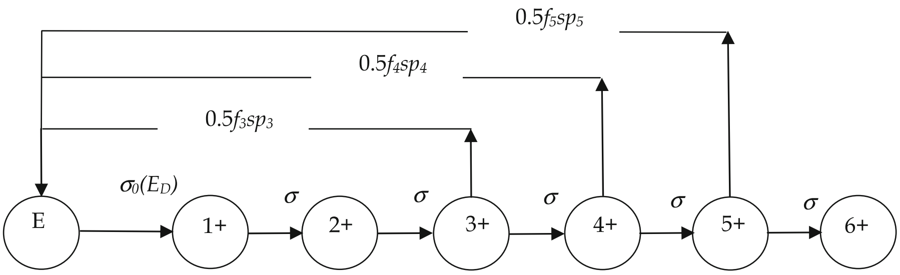

Fig. 3 Life-cycle graph of *S. marmoratus*. The survival from egg to 1+ (σ_0) is function of the density of spawned eggs (E). f_x = mean fecundity of females aged x; sp_x = spawning probability of marble trout females aged x; σ_x = annual probability of survival of marble trout from age x to $x + 1$; $\sigma_0(E_D)$ = density-dependent first-year survival; E_D = density of eggs produced. Parameters values are reported in Table 3

been estimated, we simulated 1,000 population trajectories (replicates) of 100 years each. We drew the values of model parameters at each time step of the simulation time from a uniform distribution over their respective range of variation (Table 3). For each simulation, we set the initial population abundance to 500 marble trout aged 1+, corresponding to the actual number and age of marble trout introduced in Gorska and in Zakojska in 1996. We ran simulations under three different scenarios, namely: (1) occurrence of both moderate and severe floods (Scenario SF); (2) occurrence of only moderate floods (Scenario MF); and (3) no flood events (Scenario NF). Environmental stochasticity, apart from the high-amplitude stochasticity of the flood events, was all included in marble trout vital rates. For each scenario, we computed: (a) mean number of marble trout aged ≥1+ over the simulation time and (b) the quasi-extinction risk, that is the probability of going below a threshold in population size ranging from 0 to 100 individual during the simulation.

To assess the relative importance of model parameters on population viability, we used the sensitivity analysis approach proposed by McCarthy et al. (1995). Two response variables were used for the sensitivity analysis, namely: (1) the mean population size over the simulation time and (2) a binary variable set to 1 if the population size dropped below the quasi-extinction threshold (in this case fixed at 30 individual aged ≥1+, the lowest number of marble trout found in a viable and monitored population, Huda Grapa, Fig. 1) during the simulation and 0 otherwise. We performed ordinary regression with normal error structure on the data set when the response variable was mean population size over the simulation time. We used logistic regression to explore the relationship between the probability of quasi-extinction (response variable) and model parameters (independent variables). The relative importance of each model parameter was given by its standardized regression coefficient, which was then divided by the largest absolute value of the standardized regression coefficients for that stream (Mccarthy et al. 1995). Parameters values for the sensitivity analysis are reported in Table 3. Full details on the matrix model can be found in Vincenzi et al. (2008a).

Individual-based model

We designed an individual-based model of population dynamics incorporating life-history traits and compensatory responses of marble trout and the occurrence of flood events. We parameterized the IBM separately for the populations of Gorska and Zakojska.

We developed the IBM primarily to assess the effects on the risk of quasi-extinction of two alternative assumptions on body growth trajectories: in the first case, we modelled body growth as density-dependent (Vincenzi et al. 2007b). This scenario will be referred to as DD. In the second case, we modelled body growth as density-independent. In this case, we computed mean body size at age x via the density-independent Von Bertalanffy growth function estimated for Gorska and Zakojska, respectively (Vincenzi et al. 2007b). We refer to this scenario as VB.

As we hypothesized that density-dependent individual growth increases the resilience of marble trout populations to drop in population size caused by an exogenous event (such as a severe flood), we ran simulations in which the effect of floods on population

Table 3 Model parameter values and their range of variation for the Zakojska and Gorska marble trout populations

Parameter	Zakojska		Gorska		Description
	Exp.value	Min–max	Exp.value	Min–max	
a	0.084	0.074–0.093	0.034	0.024–0.044	Parameters of the density-dependent first-year survival function
γ	0.75	0.65–0.85	0.66	0.56–0.76	
$\sigma_1 \ldots \sigma_5$	0.57	0.53–0.62	0.61	0.57–0.65	Adult survival
sp_3	0.62	0.5–0.7	0.81	0.7–0.9	Age-specific spawning probabilities used in the matrix model
sp_4	0.94	0.9–1	0.95	0.9–1	
sp_5	0.20	0.1–0.3	0.20	0.1–0.3	
f_3	106	88.4–123.60	142.80	113.92–171.68	Age-specific fecundities (# eggs per females) used in the matrix model
f_4	188	162.40–213.6	281.28	247.76–314.8	
f_5	283.62	250.62–316.62	460.70	438.76–482.64	
T_1	–	50–100	–	50–100	Recurrence interval of floods in the matrix model
T_2	–	10–20	–	10–20	
r_1	–	60–90	–	60–90	Percentage of marble trout dying after floods in the matrix model
r_2	–	10–40	–	10–40	
n_o	500	100–1,000	500	100–1,000	Marble trout stocked (aged 1+)
L_∞	318.24	294.69–351.27	376.76	345.75–418.66	Parameters of the Von Bertalanffy body growth function used in the IBM (Vincenzi et al. 2007b)
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	1.04−0.09	Parameters of the model of density-dependent individual growth used in the IBM
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	
α	−750	−925 to–525	−750	−925 to−525	Parameters of the model of egg production used in the IBM
β	3.8	2.45–5.15	3.8	2.45–5.15	

Density-independent Von Bertalanffy growth model is in the form $L_x = L_\infty\left(1 - e^{-k(x-x_o)}\right)$, where L is length (mm) of fish, x is age (years) , L_∞ (mm) is maximum length, k is Brody's growth coefficient (y^{-1}) and x_0 (y) is the age at which length equals zero. For both models of population dynamics (matrix model and IBM), values of the parameters were drawn at each time step from the uniform distribution over their respective range of variation. The same range of variation was used for the sensitivity analysis of the matrix model

abundance was explicitly accounted for. In this case, differently from what we did with the matrix model, the effect of floods on population abundance was further refined and modelled through a non–linear fuzzy function linking October rainfall to a flood-induced mortality factor F, ranging between 0 for low discharges to $F_{\max}$ (0.7, corresponding to a reduction of 70% of population size) for major flood events (Vincenzi et al. 2008b).

We ran the IBM for the population of Gorska and for the population of Zakojska for 1000 replicates of 100 years each for each of the two scenarios (i.e., VB and DD). The values of model parameters were drawn at each time step of the simulation time from a uniform distribution over their respective range of variation (Table 3).

The main output of the simulation analysis was the estimation of quasi-extinction risk for the reintroduced populations, that is the probability that adult population size drops below a given threshold ranging between 0 and 100 individuals. Full details about the IBM are reported in Vincenzi et al. (2008b).

Main results

Values of demographic and life-history traits, compensatory responses and parameters of the models of population dynamics are reported in Table 3.

Fecundity

We found a significant linear relationship $F(L) = \alpha + \beta$ between body length L and number of eggs $F(L)$ produced by a female. Although the relationship between female size and number of eggs in salmonids usually follows a power law (e.g., Lobon-Cervia et al. 1997), AIC selection on candidate models with different functional forms indicated the linear model as the best-fitting functional form.

Paternal analysis showed as minimum and maximum age for spawning for marble trout females 3 and 5 years old, respectively. First spawning occurs at a minimum length of 200 mm. All females aged 3+ and 4+ and exceeding 200 mm seem to spawn successfully. Approximately 20% of marble trout females aged 5+ spawn successfully, with probability of spawning independent of body length.

Survival probabilities

We estimated the annual survival probabilities of marble trout born in Gorska and Zakojska aged $\geq 1 + \sigma_x$ (x = 1+ $\cdots$ 5+) separately for each stream. Length and weight of marble trout did not predict survival at any age (GLM, $p > 0.05$ for all ages). Annual survival of stocking material was lower than that of trout born in the stream in both Gorska and Zakojska.

Density-dependent first year survival

We found a significant effect of density of eggs (E_D) on survival from eggs to age 1+ (σ_0) in both Gorska and Zakojska populations, well described by a negative power law curve in the form $\sigma_0 = aE_\mathrm{D}^{-\gamma}$ (Vincenzi et al. 2007a).

Density-dependent body growth

Individual growth rates ($G_{Lx} = \ln\left(\frac{L(x+1)}{L(x)}\right) x = 1 + \ldots 4+$) were well described by the linear model:

$$G_{Lx} = \mu + \beta_x x + \beta_{D_u} D_U + B_{L_\mathrm{T}} L_\mathrm{T} + \beta_{D_x} D_x$$

where x is the age of marble trout (categorical variable), D_U is total density of marble trout aged $\geq 1+$ when the marble trout was in its first year of life and D_x the total density of marble trout aged $\geq 1+$ when the marble trout is aged x (Vincenzi et al. 2007b).

PVA and sensitivity analysis of the Leslie matrix model

Averages of mean population size across replicates were substantially lower with Scenario SF while quasi-extinction risk was clearly higher (Figs. 4, 5). Quasi-extinction risk was remarkably higher under the Scenario SF than in the other two scenarios (MF and NF) over all the range of quasi-extinction thresholds (Fig. 4b, c). Simulations showed that quasi-extinction risk is systematically larger in Gorska than in Zakojska (Fig. 4b, c).

For both mean population size and quasi-extinction probability, model results were most sensitive to the strength of density-dependent first-year survival (Fig. 6). The percentage reduction r_1 of population size due to severe floods greatly affected quasi-extinction probability but not mean population abundance over simulation time, while the recurrence interval of floods (T_1 and T_2) played only a marginal role for both the response variables (Fig. 6). Similarly, the initial number of marble trout introduced in the stream did not influence either response variable in the range of size of stocking cohort considered (from 100 to 1,000 individuals aged 1+).

PVA of individual-based model

Figure 5 shows examples of simulations performed using the individual-based model (IBM) of population dynamics. The probability of quasi-extinction was substantially lower when individual growth was density-dependent (DD scenario) both in Zakojska and in Gorska (Fig. 7). When growth was density-dependent,

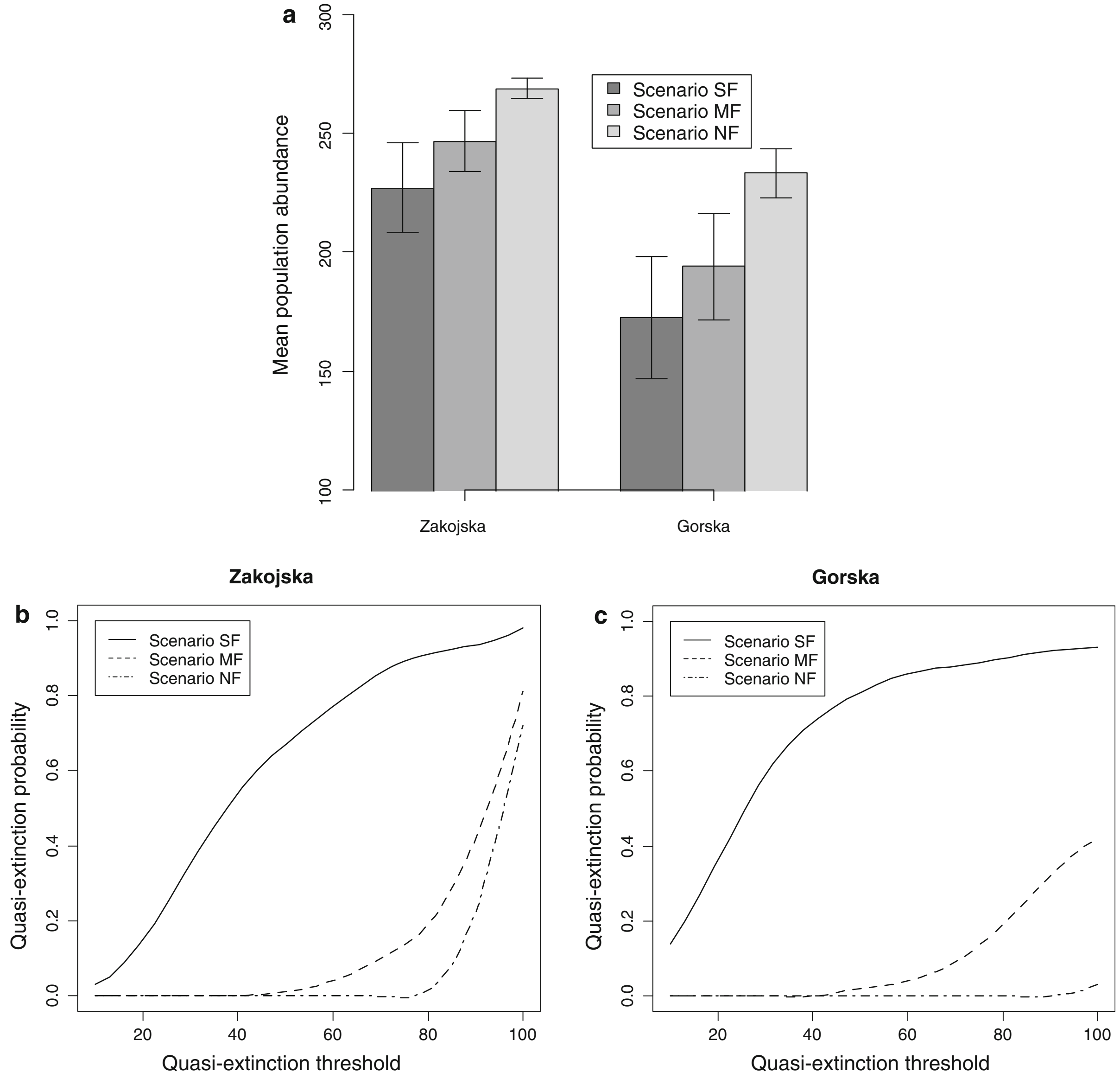

Fig. 4 **a** Mean population size and **b**, **c** quasi-extinction risk for the three scenarios simulated using the matrix model of population dynamics. *SF* severe and moderate floods, *MF* moderate floods and *NF* no floods. Quasi-extinction risk is clearly higher for both populations in scenarios with the occurrence of both severe and moderate flood events (Scenario SF). Reprinted by permission from Elsevier Science

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 (DD scenario). We observed an increase in mean length of marble trout after the 2004 flood event 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) showed a significant difference ($p < 0.05$), with marble trout sampled after the flood presenting greater mean length (2004: $n = 77$, $L_T = 107.05 \pm 14.82$; 2005: $n = 64$, $L_T = 118.55 \pm 23.70$).

Discussion

Assessing the viability of fish populations and how habitat, life-histories and demographic traits affect

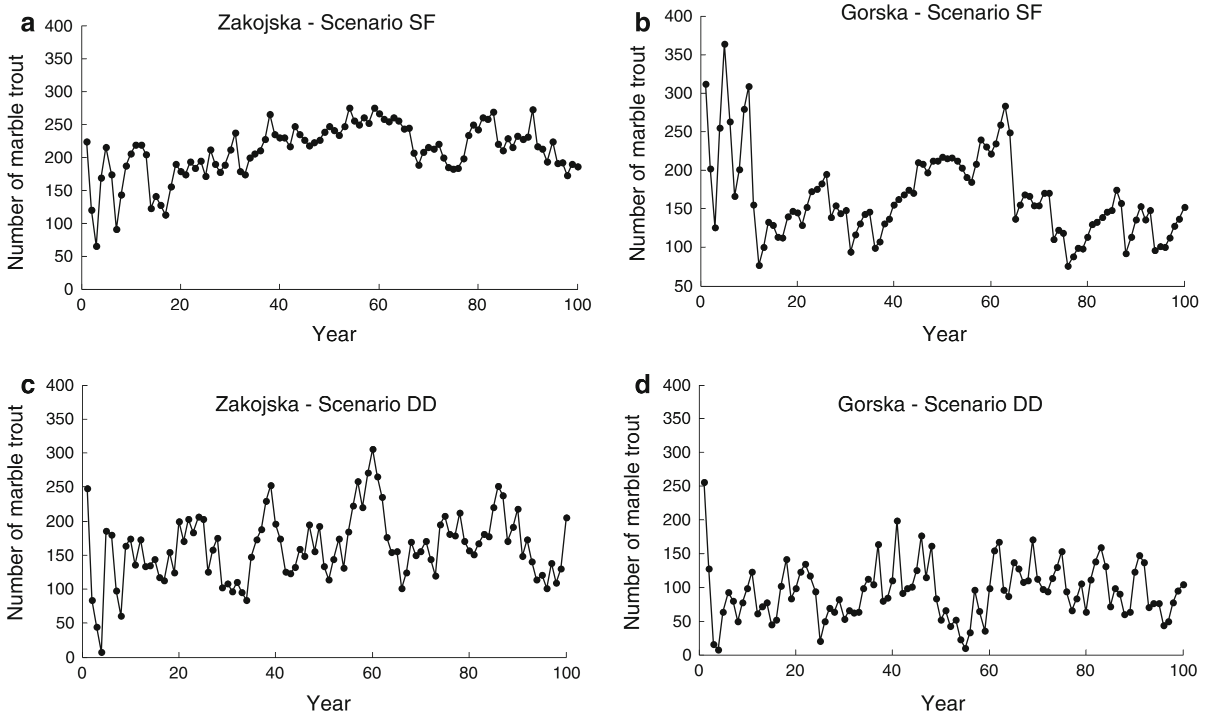

Fig. 5 Single simulation replicates representing the time-varying number of marble trout for (**a**, **b**) the matrix model of population dynamics (Scenario SF, both severe and moderate flood events); (**c**, **d**) the individual-based model (IBM) of population dynamics (Scenario DD, density–dependent body growth)

their dynamics and persistence is a major problem in fish ecology. The risks of extinction for salmonid populations are typically multi-factorial and only the results and insights of long-term programs can help elaborate measures to mitigate extinction risks, since insights from theoretical models alone are usually not sufficient to guide conservation measures. In addition, since procedures and effects of translocations are so poorly known for the vast majority of species, all techniques should be considered experimental. As a consequence, specific management recommendations should only be made after careful research on species characteristics and specific habitat conditions.

Our work helped unravel the contribution of environmental and endogenous factors for both establishment and persistence of the reintroduced populations, as discussed in detail hereafter.

Population establishment

500 trout aged 1+ successfully established marble trout populations in Gorska and Zakojska. Given the technical difficulties and monetary costs of rearing trout in fishing farms, it is important to assess whether fewer fish might be used for the future reintroductions, since the numerical reduction of the stocking cohort may provide a substantial support to the conservation efforts. The few notable examples of successful fish conservation projects–mostly concerning Atlantic salmon–have involved considerable investment in financial terms and human resources (Cowx and Collares-Pereira 2002), and reducing monetary expenses can make further conservation efforts achievable. While it might be theoretically possible to experimentally manipulate the size of the release group to empirically obtain information on the optimal composition of the stocking cohort (e.g., Berggren 2001), such experiments may require multiple reintroduction attempts and are unlikely to be feasible or recommended with threatened species. A better and more rational approach is to apply models of population dynamics, where the main life-history and demographic traits have been estimated for the species and system in question (e.g. McCallum 1994; Towns and Ferreira 2001).

Our analyses showed that stocking more than 100 individuals would not substantially increase the

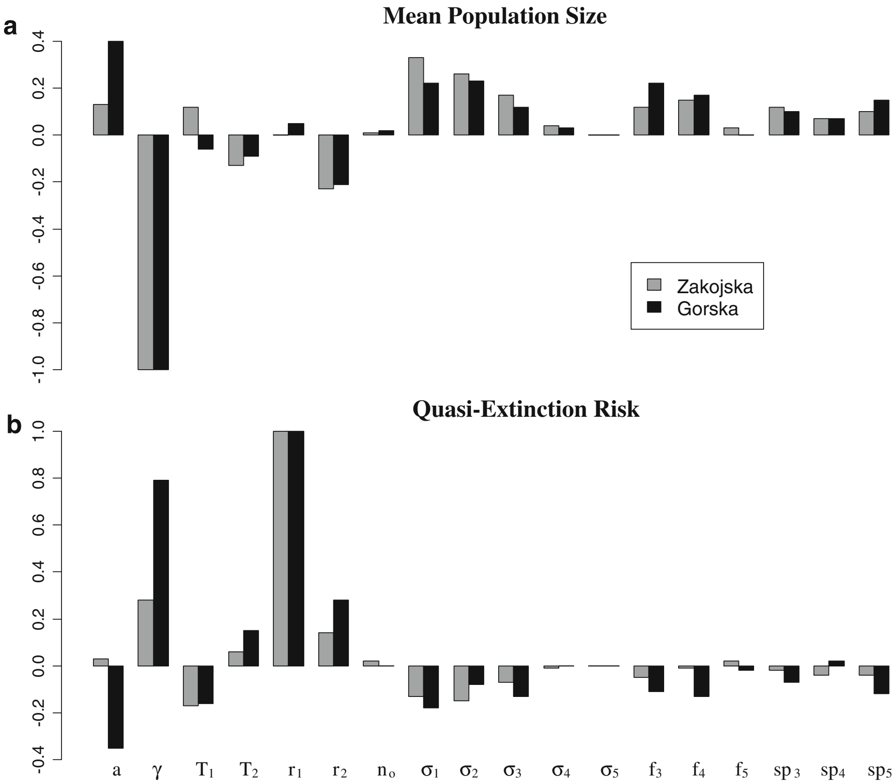

Fig. 6 Standardized regression coefficients estimated with the sensitivity analysis of the matrix model of population dynamics for the marble trout population of Gorska and Zakojska. Response variables were **a** mean population size over the simulation time and **b** risk of quasi extinction (binary variable with 1 representing population dropped below 30 individual during simulation time). See text and Table 3 for notation

chance of the establishment of the reintroduced populations, since neither mean population size nor probability of quasi-extinction were affected by the number of fish aged 1+ initially stocked in the stream when this exceeded 100 marble trout. Therefore, we argue that the number of marble trout aged 1+ introduced in both streams in 1996 (i.e., 500) could have been reduced without serious consequences for the viability of the populations, since compensatory responses in marble trout quickly regulate population size near stream carrying capacity.

Understanding regulatory processes is essential for the enlightened management of endangered species. There is ample evidence of density-dependent regulation in stream-dwelling salmonid populations (e.g., Elliott 1994; Milner et al. 2003) and early density-dependent survival is a commonly found (e.g., Elliott 1994). The density-dependent mortality in the early stages of life (within 30–70 days after emergence) is believed to be the result of strong competition for territory by newly emerged fish (e.g., Chapman 1966; Le Cren 1973; Allen 1969; Elliott 1990; Grant and Kramer 1990; Elliott 1994).

As for body growth in salmonids, studies on brown trout (e.g., Crisp 1993; Newman 1993; Jenkins et al. 1999; Lobon-Cervia et al. 1997), Atlantic salmon *Salmo salar* (e.g., Imre et al. 2005), coho salmon *Oncorhynchus kisutch* (Hartman and Scrivener 1990) showed that body growth is often density-dependent. Several works suggest that this might be a general bottom-up regulating mechanism for stream-dwelling salmonid populations (e.g., Jenkins et al. 1999; Imre et al. 2005; Vincenzi et al. 2008a). Our analysis confirmed that this is certainly the case also for marble trout. In addition, early density has long-lasting consequences (Vincenzi et al. 2007a, b, 2008a, b), since the density experienced during the first growth period affects the lifetime body growth trajectories of marble trout (i.e., carry-over effect of early environment on future growth). As the number of eggs produced by a mature female marble trout is positively correlated with body size, the lower the population density experienced as juveniles, the larger the adult body size and the higher the potential reproductive output.

The high egg production with respect to the limited availability of suitable micro-habitat for juveniles and

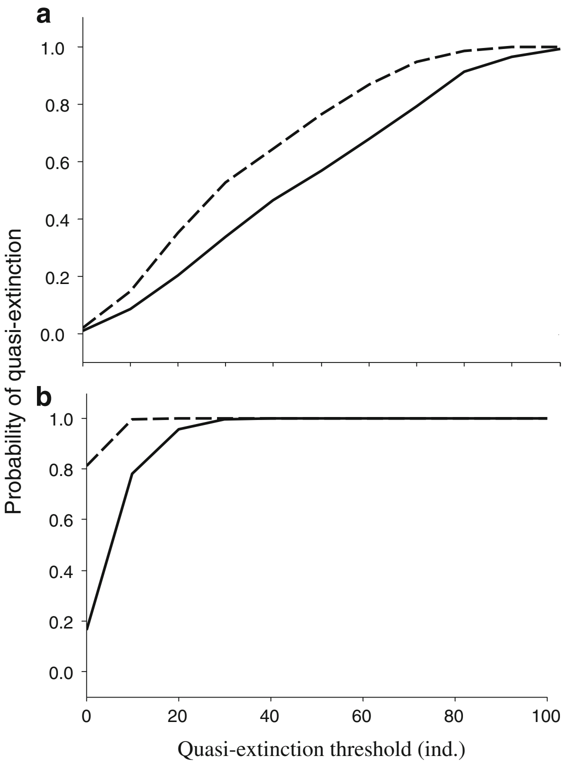

Fig. 7 Quasi-extinction risk for the marble trout populations of Gorska and Zakojska using the individual-based model (IBM) of population dynamics. *Solid line*, scenario DD (density-dependent body growth); *dashed line*, scenario VB (density-independent Von Bertalanffy body growth)

the compensatory responses (density-dependent first-year survival and body growth) are likely to regulate population size around the stream carrying capacity in a few years after the creation of the population. 0.15–0.3 ind. m^2 of stream pool surface (we tend to use pool surface as a measure for density, as total stream surface is more variable and dependent on hydrological conditions) should be sufficient to establish a population of marble trout.

However, some caution is necessary before unquestioningly follow our management recommendations, since other factors need to be considered, aside from genetic considerations (Armstrong and Seddon 2008). Depending on the purpose of stocking and economic constraints, age classes of introduced fish, time and place of release vary accordingly (see Sarrazin and Legendre 2000 for a comprehensive approach). Large scale captive breeding and release programs have many genetic and life-history implications that should also be carefully considered (Seddon et al. 2007). Maladaptation of hatchery fish to the natural environment is a common occurrence which may be reflected in a variety of life-history traits, and be based on developmental and/or genetic factors (Kleiman 1980; Frankel and Soule 1981). It has been observed that stocked fish experience high initial mortality, due to both biotic and abiotic factors (Berg and Jørgensen 1991, Vincenzi et al. 2008a). The survival of stocked fish is likely to be regulated in a similar manner as for newly emerged fry (Berg and Jørgensen 1991) and with also the contribution of prior residence effect (i.e., Deverill et al. 1999). Vincent (1960) showed that hatchery raised brook trout *Salvelinus fontinalis* had less stamina, lower survival rates, less fright response, and less tendency to conceal themselves than wild individuals. Hatchery fish may produce maladapted offspring subject to different levels of selection pressure towards the optimum phenotype (for a recent and comprehensive review see Fraser 2008). However, Armstrong and Seddon (2008) cautioned that comparative analyses of reintroduction success rates for multiple species and systems may give a misleading indication of the relationship between composition of release group (i.e., size and age) and establishment success, since low numbers are generally released when the chances of success of the reintroduction are deemed to be poor, thus creating a bias in favour of larger release groups.

In light of the previous creation of Zakojska and Gorska populations, managers of MTCP decided that new reintroductions of marble trout would be carried out by planting eyed-eggs in artificial redds. Such a technique increases the selection pressure in the early stages of life and is thus likely to increase the loss rates of maladaptive traits of trout raised in captivity. Since 2006, three new pure marble population were created in the same region (Martinkov Potok, Kokosnjak and Plascak) by planting eyed-eggs in artificial redds and preliminary explorations show an increased early selection of favourable traits (Dusan Jesensek and Alain J Crivelli, unpublished data). This is a clear example of adaptive management in conservation (Armstrong et al. 2007).

Population persistence

The simulation analyses supported the hypothesis that marble trout populations are remarkably stable in the absence of flood events and surprisingly resilient to severe floods (Fig. 4), assuming that suitable spawning habitat remains available after the disturbance event. We want to stress that one of the peculiarities of MTCP is the remoteness of the streams where marble trout live and the consequent absence of relevant anthropogenic disturbance (i.e., habitat alteration, water pollution etc.). On the contrary, the risk of deterministic extinction of salmonids is likely to be greater in more disturbed and less pristine streams (Rieman et al. 1993). In those disturbed environments, limited availability of pools and woody debris for overwintering, the degradation of spawning habitats and habitat fragmentation are major threats to population persistence.

Using the matrix model, with both severe and moderate floods (Scenario SF) quasi–extinctions happened generally after a severe flood event. Quasi-extinction probability was greater in Gorska than in Zakojska across scenarios and models of population dynamics, since with a lower carrying capacity the population of Gorska population was more likely to drop below the quasi-extinction threshold. The sensitivity analysis on model parameters also showed that density-dependent first-year survival is the most important endogenous factor for population size at quasi-equilibrium (Fig. 6). Our interpretation is that the availability of suitable habitat for juvenile marble trout–which is well correlated with the physical complexity of the stream bed–probably acts as a bottleneck with respect to population size. This further encourages management actions to preserve suitable micro-habitat for juveniles.

Simulations with the IBM showed that density-dependent body growth and density-dependent first-year survival may allow a faster recovery after population collapses and thus lower the risk of quasi-extinction (Fig. 7). After severe flood events (assuming suitable habitat remains), individual growth of surviving juvenile and adult individuals increases thanks to the reduction in density-dependent intra-specific competition. Females are thus expected to be larger at sexual maturity and/or to reach maturity faster, and to produce more eggs per-capita. The increased fertility combined with the increase in density-dependent first-year survival at low densities allows the surviving population to recover faster than in case of no effects of density on body growth, thus reducing the “acute” risk of extinction following a massive mortality event. Increased body growth rates have been observed for juvenile and adult salmonids areas after severe disturbance events (Elwood and Waters 1969; Lamberti et al. 1991; Letcher and Terrick 1998) and we hypothesize that natural selection in highly variable environments like Slovenian mountain streams should have favoured a general tendency toward *r* strategies facilitating rapid rebounds after “wash-out” effects (Vincenzi et al. 2011b).

Density-dependent body growth has relevant implications also for the development and application of models of population dynamics and population viability analysis. Since density-dependent body growth had important consequences for population regulation in absence of flood events and resilience to drops in population size, management and conservation plans based primarily on matrix model projections and elasticity analyses should be approached with caution. Large fluctuations in population densities, as commonly observed in stream-dwelling salmonids, could affect both individual growth and age at maturity (assuming that body size at sexual maturity does not co-vary with age) and may lead to compensatory changes in life-histories through phenotypic plasticity or genetic adaptations. Therefore, the results and perspective provided by models of population dynamics in matrix form may not reflect the outcomes of management actions and thus putting at risk the conservation efforts.

In synthesis, only severe disturbance events seem able to trigger local extinction of populations, otherwise marble trout are quite persistent and able to recover even after massive mortality events. Flood intensity is strongly affected by stream and watershed features such as morphology, soil type and texture and presence of vegetation. This might explain why Gorska, with its high slope and absence of flood plain, was fishless before the introduction. In 2005 we conjectured that even the marble trout population of Zakojska, which was fishless before the creation of the new population in 1996 and declined considerably after the October 2004 flood (but quickly recovered), would eventually disappear after a major flood. The flood of September 2007 that wiped out more than 95% of the individuals seem to have confirmed our prediction. If the four fish sampled in Autumn 2010 (two males and two females) did not reproduce successfully in autumn 2009 and 2010, the population will be extinct in 2011–2012. The next sampling survey will allow us to assess whether the population was able to recover or not.

Stochastic factors and long-term viability

Stochastic abiotic processes causing rapid drops in population size (i.e., floods, droughts, landslides) may have posed little threat to most local and regional salmonid populations in the past (Rieman et al. 1993). However, with the loss of habitat and fragmentation that occurred in the last century, many populations declined dramatically in size and have been restricted to marginal or highly variable habitats. This increases the risk of extinction from stochastic abiotic factors and the need of larger areas to support self-sustaining population in the face of demographic and environmental stochasticity. Habitat change can influence not only the amount of environmental variation, but also the sensitivity of a population to that variation. Natural or artificial barriers, while often protecting native species from upstream migration of non-native salmonids (Vincenzi et al. 2011a), restrict populations to areas potentially too small to support a viable population (Moyle and Sato 1991; Moyle and Yoshiyama 1994). In addition, identifying minimum habitat requirements (e.g., Harig and Fausch 2002) and minimum viable population may become problematic in presence of large stochastic events (Flather et al. 2011), since floods and debris-flows affecting whole streams can suddenly “wash out” even more abundant populations than those created within MTCP.

Changing climate trends along with climate change-induced intensification, altered frequency and seasonality of weather extremes pose additional threats to freshwater fish species and increase the risk of species-level extinctions (Thomas 2011). The role of extreme flood events on the demographic fate of marble trout in these pristine habitats is likely to increase as a consequence of the on-going global climate change. According to IPCC model projections for the twenty-first century, frequency of extreme flood events is expected to increase in the next 50 years (IPCC 2007) and recent evidence and studies seem to support model predictions (Min et al. 2011; Pall et al. 2011). Moreover, hydrologists–through recent advancement in the statistical theory of extreme events-, have shown that the return times of large floods even in absence of climate change are markedly shorter than expected (what was considered the 500-year flood is actually the 50-year flood, Katz et al. 2002). This suggests that the consequences of flood events on population dynamics and life-histories of freshwater salmonids, and on environmental shifts, habitat modifications and altered connectivity for meta-populations, deserve particular attention and that in pristine environments, low-frequency, but high-amplitude environmental stochasticity will become relevant greater risk factor for those populations.

The sensitivity analysis indicated that first year survival linked to juvenile carrying capacity of the stream and the reduction in population size after a severe flood are the two most important factors limiting the persistence of the reintroduced populations. In the paradigmatic case of marble trout, fishless headwaters are not recommended for the reintroductions. A posteriori we can confidently assert that Gorska and Zakojska–streams in remote areas where poaching activities can be excluded–were fishless due to the repeated occurrence of severe flood events. The steep slope of the stream bed with few hides combined with the very steep slope of the catchment (Table 1) contribute to intensify the effects of the floods. Our experience greatly recommends the careful examination of stream and watershed features of the site of translocation to avoid the selection of sites subject to brief and violent alterations of the hydrological regime. Thus, we suggest that whenever possible reintroductions should be undertaken at lower altitudes, where no fish are present upstream and where the upstream movement of possibly hybrid fish is prevented by natural or artificial barriers.

Acknowledgments The Marble Trout Conservation project was mainly by the Foundation MAVA throughout its duration. The authors thank all the people who participated to the fieldwork since 1993.

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