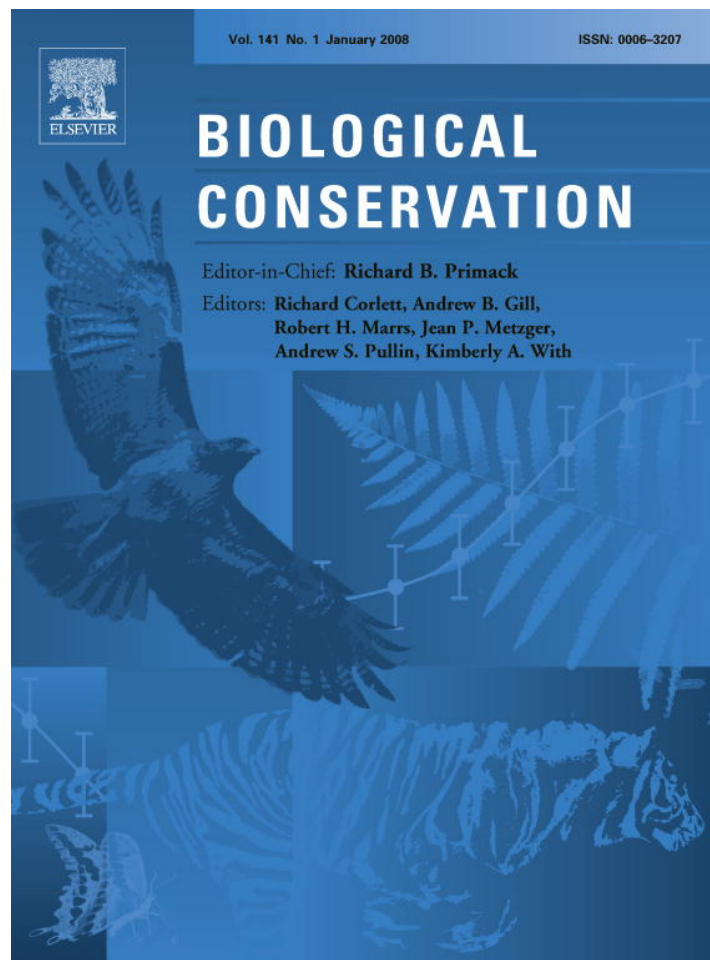


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Potential factors controlling the population viability of newly introduced endangered marble trout populations

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ABSTRACT

While several population viability analyses (PVAs) have been performed on anadromous salmonids, less attention has been given to stream-living salmonids. In this work, we explore the role of PVA as a tool in the recovery of threatened stream-living salmonid species. The analysis has been performed with reference to marble trout *Salmo marmoratus*, a salmonid with a limited geographic distribution and at risk of extinction due to hybridization with the non-native introduced brown trout. Demographic parameters, such as survival, fecundity and density-dependent patterns were estimated from an eight year on-going monitoring program of two translocated marble trout populations in pristine, previously fishless streams (Zakojska and Gorska) in the Soca and Idrijca river basins (Slovenia). To explore the importance of disturbance events such as floods on marble trout population dynamics, we performed a PVA under three scenarios: (1) occurrence of both severe and moderate floods; (2) occurrence of only moderate floods; (3) no flood events. Our analysis shows that population viability is threatened only by severe flood events, otherwise the two populations prove to be fairly stable with population abundance fluctuating around stream carrying capacity. A sensitivity analysis performed on model parameters highlighted that density-dependence in first-year survival and the magnitude of reduction in population size after a severe flood are the two most crucial parameters affecting population abundance and quasi-extinction probability, respectively. While only extreme floods can drive the population to extinction, the increase in juvenile survival when population abundance collapses after a major flood may allow the populations to quickly recover from few reproductive individuals back to stream carrying capacity.

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1. Introduction

Population viability analysis (PVA) makes use of quantitative methods to predict the likely future status of a population or collection of populations of conservation concern (Morris

and Doak, 2002). Broadly defined, PVA is used by conservation planners to evaluate the risk of extinction over specified time intervals, the rate of population growth or indicators of population health. Despite some limitations (Reed et al., 2002), PVA is considered a valid tool for categorizing and managing

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endangered species (Brook et al., 2000). Nevertheless, a recent review by Morris et al. (2002) on the use of population viability analysis in endangered species recovery plans in the US highlights the scarce application of PVAs to support recovery efforts; only 14% of the plans approved since 1991 presented information on PVA. This is unfortunate, as PVA can greatly improve the management of threatened species (Morris et al., 2002; Lande et al., 2003) depending upon the availability of data to calibrate the demographic model. In fact, with PVA it is possible to explicitly account for both environmental variability and uncertainty in parameter estimation. Additionally, sensitivity analyses can be used to determine which specific demographic factors are most relevant in determining the demographic fate of the population. On the basis of such information, managers can evaluate the effectiveness of conservation strategies.

A number of studies concerning the PVA of endangered salmonid species have been published in the last decade, often regarding anadromous species (i.e., Ratner et al., 1997; Botsford and Brittnacher, 1998; Zabel et al., 2006). However, PVAs have been rarely performed on stream-living salmonids (e.g., Morita and Yokota, 2002) even though freshwater fishes are thought to be the world's most threatened group of vertebrates after amphibians (Bruton, 1995; Smith et al., 2006). In the present study, we used PVA to help understand the population dynamics of stream-living marble trout *Salmo marmoratus*,

and provide perspective on the creation of new populations through translocations.

The marble trout *S. marmoratus* (Cuvier) is a species of great conservation concern, given the geographical distribution restricted to the Po basin in northern Italy (Sommani, 1961; Forneris et al., 1990), the Adriatic basin of Slovenia, Croatia, Bosnia-Herzegovina (Povz et al., 1996) and Albania (Schoffmann, 1994) and the risk of hybridization with brown trout *Salmo trutta* L. Since the beginning of the last century, brown trout were introduced for commercial and recreational purposes in the geographic region where *S. marmoratus* is endemic, quickly leading to the creation of hybrid populations (Giuffra et al., 1996; Berrebi et al., 2000). Presently, only seven remnant pure populations of marble trout are located in the Adriatic basin of Slovenia (Fig. 1, the Predelica population went extinct in year 2000) (Berrebi et al., 2000; Fumagalli et al., 2002) persisting above barriers preventing the upstream movement by conspecifics. Therefore, there is no potential for spontaneous colonizations of new habitats through dispersal or re-colonization after local extinctions.

The Marble Trout Rehabilitation Project started in 1993 in the upper basin of the Soca river (Slovenia) (for details refer to Crivelli et al., 2000); the project goals included the duplication of the existing pure populations through translocation of marble trout in fishless streams to enhance the long-term viability of the species (Crivelli et al., 2000). Translocation of

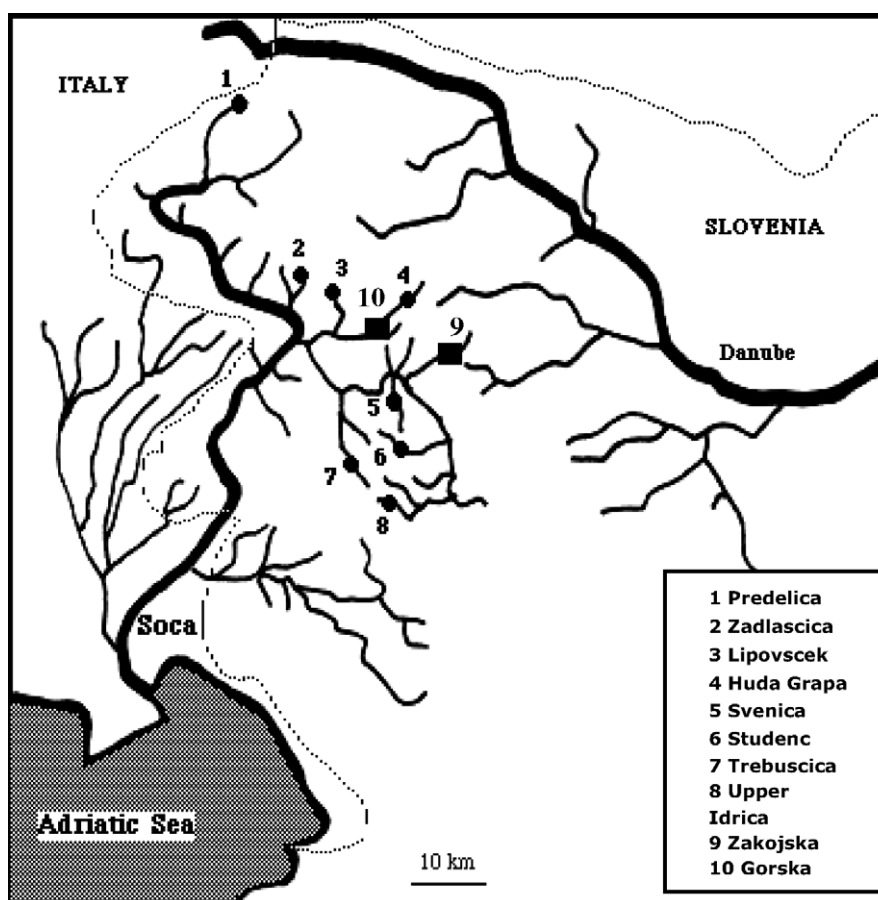


Fig. 1 – Location of *S. marmoratus* populations within the Soca and Idrijca river basins in Slovenia. The Soca and Idrijca river basins lie in the western part of Slovenia and belong to the Adriatic basin.

individuals to establish, re-establish or supplement a population is a fundamental strategy in the conservation of endangered or threatened species. At least 80% of recovery programs for fish (Williams et al., 1988) suggest translocations as an effective means to enhance the viability of the species under recovery. Despite some highly-publicized successful translocation programs (e.g., America Bison (*Bison bison*), Kleiman, 1989; Peregrine Falcon (*Falco peregrinus*), Millsap et al., 1998) the success rates for translocations of birds, mammals and fish are generally low (Williams et al., 1988; Griffith et al., 1989; Simons et al., 1989; Hendrickson and Brooks, 1991; Harig et al., 2000). As only a few rehabilitation projects implement a monitoring scheme after the translocations have occurred, the cause of low success rates of translocations often remain unknown. This demonstrates the need for a quantitative assessment of the ecological factors which have the major influence on the effectiveness of translocation projects.

In this work we present a PVA for two translocated pure marble trout populations living in two streams (Gorska and Zakojska) in the Soca and Idrijca river basins (Slovenia). Specifically, we estimated the demographic parameters and density-dependent patterns of marble trout, which were then used to define a Leslie transition matrix (Caswell, 2001) for marble trout population of Gorska and Zakojska. A stochastic demographic model for marble trout that accounted for uncertainty in the estimation of demographic parameters was also developed, to investigate the importance of exogenous environmental factors in determining marble trout population dynamics. We used the model to estimate population viability – in terms of mean population size and probability of quasi-extinction – by explicitly including the role of flood events on population abundance and persistence. A sensitivity analysis was performed to identify the relative importance of vital rates and the frequency and intensity of flood events on mean population size and quasi-extinction risk. On the basis of these analyses we derive some insights for the translocation and management of pure marble trout populations, in terms of selection of suitable sites and size of stocking material when creating a new population in a previously fishless stream or in streams where depletion-removal electrofishing has occurred (Thompson and Rahel, 1996). Finally, we discuss the role of population viability analysis in conservation projects of freshwater salmonid species.

2. Material and methods

2.1. Study area

The Soca and Idrijca 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. Fly fishing taking place in the lower part of the rivers is one of the main attractions for tourists, attracting many anglers from abroad, and among the most profitable economic activities in the region (Sullivan et al., 2003).

Marble trout is the only fish species present within both the experimental streams (Gorska and Zakojska), located in headwaters and with no predation or fishing activities.

Stream length and topographic features were acquired from field investigations and from available geospatial datalayers (source: Surveying and Mapping Authority of the Republic of Slovenia). Habitat features of Zakojska and Gorska are presented in Table 1. Both studied streams are one-way streams, Gorska stream being more fragmented (11 sectors) by natural waterfalls – which prevent the movement of the fish upstream through the barrier – than Zakojska (7 sectors). Average length of sectors is longer in Zakojska (177 ± 41 m) than in Gorska (76 ± 38 m). The stream bed of Gorska consists mostly of bedrock slides, with few shelter areas and minimal floodplain. Zakojska has a wider stream bed and in case of flood can overflow its bank on a wide area of riparian forest potentially creating new suitable habitat for marble trout.

Rainfall data have been acquired since 1961 (ARSO, Environmental Agency of Slovenia). The annual mean precipitation is 2400 mm with October and November presenting the highest monthly precipitations. Annual rainfall for the study period varied little across years, ranging from 1764.5 mm in 2003 to 2495.7 of 2000. In contrast, monthly rainfall showed up to 500-fold variation for March ranging from 0.9 mm during the severe drought of 2003 to 479.5 mm of 2001. In April, a 3-fold variation was observed during the study period, ranging from 119.7 mm in the 2002 to 362.8 mm in 1999.

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

Marble trout have highly plastic individual growth rates; individuals of up to 25 kg have been found in the lower reaches of the Soca river (Fumagalli et al., 2002) while in experimental streams the maximum weight recorded was 520 g. In the study area, maximum age recorded for marble trout was six 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

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

Main features	Zakojska	Gorska
<i>Watershed characteristics</i>		
Watershed area (m ²)	62,600	21,900
Stream length (m)	2480	1940
Land average slope (%)	60.65	64.35
Surface stream average slope (%)	22.5	22.8
<i>Experimental stream characteristics</i>		
Length (m)	1238	845
Surface area (m ²)	3544	1805
Pool surface (m ²) (% of total surface)	895 (25.3)	685 (38)
Altitude range (m a.s.l.)	578–728	400–514
Number of sectors	7	11
Benthos biomass (mg m ⁻²)	14,638	11,446
IBGN (water quality class) ^a	16(2)	15(2)

^a IBGN: Indice Biologique Général Normalisé (water quality class: 1 = pristine to 5 = very polluted).

occurring in April–May. Observational data in the Soca and Idrijca river basins where pure marble trout occur show evidence of a certain amount of repetition in reproduction (iteroparity).

2.2. Sampling campaign and data collection

In November 1994, wild genitors from one of the remnant pure populations (Zadlascica) were taken, stripped in the hatchery and returned to their stream. Fish produced were reared to one year and then stocked in June 1996 in two fishless streams of the Baca river basin, Zakojska and Gorska, isolated from the hybridization zone by natural impassable waterfalls. Each released individual was marked with a Carlin tag that does not affect survival and growth of marked fish (Kolari et al., 1998). Sampling was performed every June from 1996 to 2004 on the whole length of each stream starting from downstream to the upstream extent using a gasoline-powered, portable backpack electrofishing unit. Each stream was electrofished two times to produce a multiple-pass removal estimate of trout abundance using Microfish 3.0 (Van Deventer and Platts, 1989). Age designation follows standard terminology; marble trout in the first year of life were denoted as 0+ and in the second year, subsequent to winter annulus formation, as 1+. All captured fish aged $\geq 1+$ were 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. Then marble trout were returned near the point of capture. Age was determined by tag examination. At first marking, scales were taken to assess the age of the fish. The small size of marble trout aged 0+ prevented their sampling in June and therefore they were not included in this study. Sampling in June precluded the sexing of marble trout as sex of marble trout is not discernible externally at that time of the year. Marble trout hatched in the streams aged 1+ were sampled each year from 2000 to 2004 included. As no data on stream flow were available, rainfall was used as surrogate of stream discharge. Monthly rainfalls were recorded at Rut precipitation station, the nearest one available to both streams, for the whole period of the study (1996–2004).

2.3. Survival rates

A capture history representing the fate of an individual over the study period was constructed for each tagged marble trout. Two probabilities can be estimated from a capture history matrix: ϕ , the apparent survival probability, and p , the capture probability (Lebreton et al., 1992). Apparent survival represents the probability that an individual survives from year t to year $t + 1$ and does not leave the study area. Capture probability represents the probability that an individual alive in the area at year t is captured at year t . Capture history matrices were used as input files the software MARK (White and Burnham, 1999). First, we fitted capture–recapture data with the Cormack–Jolly–Seber (CJS) model in which ϕ and p are time-dependent. This model assumes that the fate of each individual is independent of the fates of all others and that all individuals have equal survival and capture probabilities. Groups of individuals can be defined and in-

cluded as factors in the model in order to reach these assumptions. The goodness of fit (GOF) was assessed using U-Care software (Choquet et al., 2003). Maximum likelihood estimates of survival and capture probabilities were computed using the software MARK with a logit link function (White and Burnham, 1999). Model selection procedure started with the general model in which survival and capture probabilities depend on year and age class. Then, simplified models were fitted; simplification was first applied on capture probabilities and then to survival probabilities using the selected capture model. Model selection was based on the Akaike Information Criterion (AIC; Lebreton et al., 1992; Burnham and Anderson, 1998). The minimum value of AIC indicates the best compromise between the fit of the model and the precision of parameter estimates. In presence of data heterogeneity detected in the GOF test, a variance inflation factor (\hat{c}) was integrated in the calculation of AIC (QAIC) and standard errors of estimates (Lebreton et al., 1992; White and Burnham, 1999). Lebreton et al. (1992) indicate that \hat{c} values less than three are acceptable without searching an alternate model.

Survival estimates were corrected by the tag loss probability estimated in the corresponding stream. The best model estimated constant annual survival across ages in both stream. Mean survival estimates for fish born within the streams along with 95% confidence intervals are reported in Table 2.

2.4. Fecundity

Fecundity rates were estimated by stripping wild females aged 3+ to 5+ captured from the Zadlascica pure marble trout population and brought to the fish farm (Tolminka, Tolmin, Slovenia) in November–December in 1998 and 1999. After being stripped and measured in weight and length, females were returned to their stream. Fecundity rates in salmonids are size-dependent and accordingly age-dependent (Todd et al., 2004). From the experiments performed in fish farm, the number of eggs produced (E) is related to total length (L_T) of female by the linear relationship $E = \alpha + \beta L_T$ ($N = 33$, $p < 0.01$, $R_{\text{adj}}^2 = 0.5$, $\alpha = -749.97 \pm 94.24$, $\beta = 3.8 \pm 0.69$). Parental analyses performed on remnant pure marble trout populations living in the study area showed minimum and maximum age for spawning for marble trout females 3+ and 5+, respectively (Meldgaard et al., 2007). First spawning occurred at a minimum length of 200 mm and at an age of three or four years old. 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. Mean age-specific spawning probabilities and 95% confidence intervals, that is the age-specific percentage of marble trout successfully spawning (Crivelli, unpublished data), are reported in Table 2. Age-specific fecundities ($\hat{E}(x)$) were estimated by following the Monte Carlo approach described in Vincenzi et al. (in press). The higher mean age-specific fecundity in Gorska marble trout population reflects the higher mean body-length growth rates of marble trout in Gorska, a consequence of the lower marble trout density in Gorska with respect to Zakojska (Vincenzi et al., 2007). Estimates of mean age-specific fecundity along with 95% confidence intervals are reported in Table 2.

Table 2 – 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	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	
$\sigma_1 \dots \sigma_5$	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
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)
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
T_2	–	10–20	–	10–20	
r_1	–	60–90	–	60–90	Percentage of marble trout dying after floods
r_2	–	10–40	–	10–40	
n_0	–	100–1000	–	100–1000	Marble trout stocked

2.5. Density-dependency of first-year survival

As noted by Milner et al. (2003) the evidence for density-dependent regulation of abundance for stream-dwelling salmonids is overwhelming. In particular, density-dependent effects on mortality act mostly during the very early stages of life (30–70 days after hatching for Elliott, 1993), after which mortality is density-independent. Accordingly, information on density-dependent survival in marble trout needed to be incorporated into the population dynamics model to develop realistic insights from model outcomes. Vincenzi et al. (in press) found a significant effect of density of eggs on survival from eggs to age 1+ (σ_0) in marble trout living in Gorska and Zakojska, defined by a negative power law curve in the form $\hat{E}\sigma_0 = a\hat{E}_D^{-\gamma}$ where \hat{E}_D is the estimated density of eggs produced. Estimates of a and γ along with the respective range of variation (95% confidence interval) are reported in Table 2.

2.6. Impact of flood events

Streams occupied by salmonid populations are subject to natural exogenous disturbances leading to changes in instream habitat (shelter, spawning grounds, etc.) and in population size. These natural events range from moderate events to more severe, catastrophic events, with recurrence intervals measured in decades or centuries (Roghair et al., 2002). Given the high temporal and spatial variability of rainfall in the study area, stream morphology and watershed features (Vincenzi et al., in press), the frequency and intensity of exogenous factors, in particular of severe floods, play a major role in determining marble trout population size and risk of extinction. Stream discharge is the major source of variation in aquatic systems (Poff et al., 1997); discharge patterns can be described by several variables grouped into five main categories: magnitude, frequency, duration, timing and rate of change in the hydrological regime (Poff et al., 1997). On one hand, the rise of water level during moderate floods can increase spawning grounds and nursery zones, but this can only occur where the stream bed is not constrained by narrow walls and the flood plain can provide suitable habitat, espe-

cially for juveniles. On the other hand, it is generally accepted that floods of high magnitude can reduce stream-living trout populations, either by flushing away adult trout or, especially in the post-spawning period, by destroying developing eggs and thus impairing recruitment (Seegrist and Gard, 1972). Flood impacts are usually greater when eggs are in the gravel or when fry are emerging (Seegrist and Gard, 1972; Hanson and Waters, 1974; Pearsons et al., 1992). The dramatic impact of severe flood events in the regulation of population size became evident in our study area in October 2004, when a flood event occurring in Slovenia streams of the Soca and Idrijca river basins with a presumable recurrence interval of 50–100 years caused a reduction in population size in all the marble trout populations ranging from 31% to 78%, from which they quickly recovered (Fig. 2). Moreover, the heavy rainfall of

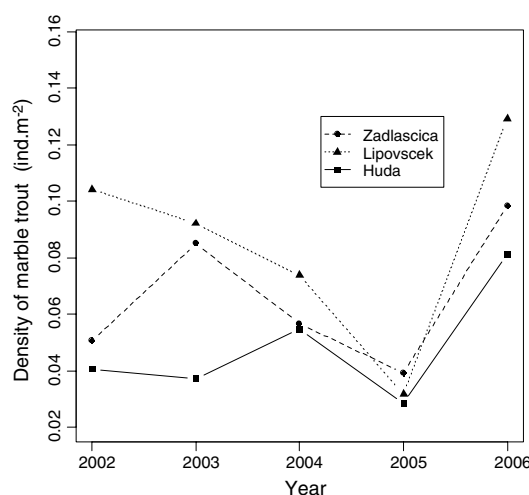


Fig. 2 – Population density over time in the remnant marble trout populations of Lipovscek, Zadlascica and Huda Grapa, estimated by dividing the number of marble trout aged $\geq 1+$ for the overall surface area of pools. The populations quickly rebounded to pre-event level after the October 2004 flood.

October 2004 induced a debris-flow in Gorska which almost completely wiped out the entire marble trout population. Although in Slovenian mountain streams the occurrence of floods during fall is common, the severity and frequency of floods vary greatly from year-to-year depending on the duration, frequency and intensity of rainfall. Local geomorphology may also play a role in the flood dynamics; brief and violent floods, which can flush trout away, typically occur in high-gradient constrained channels (i.e., Gorska). Direct measures of stream discharge are not available for the study area and thus we used rainfall as a proxy indicator.

The rainfall data and the effects of the October 2004 flood on the translocated and remnant marble trout populations in the study area seem to suggest an important role of moderate and severe October flood events in population regulation of marble trout. In absence of sufficiently long time-series of data to relate the amount of rainfall – and thus of stream discharge – in October to marble trout survival, the frequency and the impact of floods were modelled as follows. We assumed that two uncorrelated types of flood events can occur: one with a recurrence interval T_1 ranging between 50 and 100 years (October rainfall >500 mm) which causes a reduction r_1 in population abundance between 60% and 90%, that was the highest reductions in population size observed after the October 2004 flood (severe flood); and one with a recurrence interval T_2 between 10 and 20 years (October rainfall >300 mm) causing a reduction r_2 in population abundance between 10% and 40% (moderate flood). We assumed that October rainfalls <300 mm do not cause a reduction in population size.

2.7. Matrix population model

An age-classified matrix population model (Caswell, 2001) was designed to take into account the main life-history traits of marble trout described above. Eggs are produced in autumn of year t , 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 included seven age-classes, the first one accounting

for the number of eggs and the other six for marble trout aged 1+, 2+ · · · 6+. The population dynamics is described by the following matrix model (Caswell, 2001):

$$\mathbf{n}(t + 1) = \mathbf{M}\mathbf{n}(t) \tag{1}$$

where $\mathbf{n}(t) = [E(t)n_1(t)n_2(t) \dots n_6(t)]^T$ is a vector representing the number of individuals in each age-class in the population at time t and \mathbf{M} is the projection matrix (Leslie matrix, Caswell, 2001) reported in Fig. 3 along with the life-cycle diagram of marble trout living in the study area. Each non-trivial element of the projection matrix represents the transition probability from age i to age $i + 1$ (Table 2) and is time-dependent. First-year survival σ_0 from eggs to age 1+ was assumed to decrease with eggs density, as reported by Vincenzi et al. (in press).

2.8. Viability analysis

Once model parameters had been estimated, we simulated 10,000 population trajectories (replicates) of 100 years each, a reasonable time span for marble trout which in the study area have an estimated generation length of 3.5 years (Crivelli, unpublished data). The values of vital rates were drawn at each time step of the simulation time from a uniform distribution across their respective range of variation reported in Table 2. The uniform distribution was chosen to stress the variability in parameter estimates (Cross and Beissinger, 2001). For each simulation, initial population abundance was set to 500 marble trout aged 1+, corresponding to the actual number of marble trout introduced in Gorska and in Zakojnska in 1996. At each time step, the number of eggs and marble trout in each age class was estimated by using model (1) with Leslie matrix entries randomly drawn over their respective range of variation (Table 2). We ran simulations under three different scenarios, namely: (i) occurrence of both moderate and severe floods (Scenario SF); (ii) occurrence of only moderate floods (Scenario MF); and (iii) no flood events (Scenario NF). In this latter case, environmental stochasticity is all included in marble trout vital rates.

$$\mathbf{M} = \begin{bmatrix} 0 & 0 & 0 & \frac{1}{2}f_3sp_3 & \frac{1}{2}f_4sp_4 & \frac{1}{2}f_5sp_5 & 0 \\ \sigma_0(E_D) & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \sigma_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \sigma_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \sigma_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \sigma_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \sigma_5 & 0 \end{bmatrix}$$

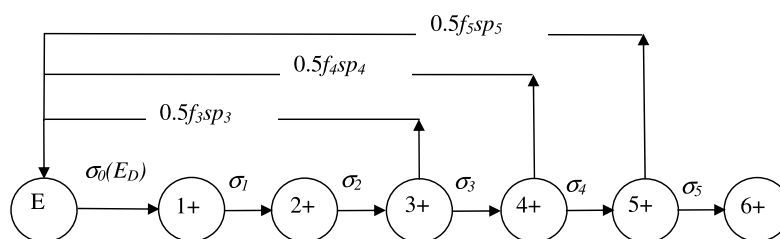


Fig. 3 – Leslie matrix of the population matrix model and life-cycle graph of *S. marmoratus*. The survival from egg to 1+ (σ_0) is function of the density of spawned eggs.

The recurrence interval of severe and moderate flood events, T_1 and T_2 , respectively, and the corresponding reduction in population abundance r_1 and r_2 [$0 < r_i \leq 1$] were drawn randomly at the beginning of each 100-years simulation from a uniform distribution across their range of variation, as illustrated in Table 2. Then, to determine the occurrence of floods, a random number x between 0 and 1 was drawn at each time step: if $x < 1/T_i$ ($i = 1, 2$) there was no flood, otherwise a flood event was assumed to occur with a consequent reduction in population abundance equal to r_i . No correlation structure was assumed for the frequency of events and the corresponding reduction in population size.

Based on the 100-year simulations, we calculated two measures of population performance. First, we estimated the quasi-extinction risk, that is the probability of adult population abundance ($\sum_{i=1+}^{6+} n_i$, where n_i is the number of marble trout in each age class) to drop below a given threshold of population size. As picking up a single quasi-extinction threshold would be debatable (Ludwig, 1999), we computed the probability of quasi-extinction with different quasi-extinction thresholds ranging between 10 and 100 individuals. The probability of quasi-extinction was thus estimated as the proportion of the 10,000 replicates in which the population abundance fell below the threshold at least one time during the 100-years simulation time.

Second, we computed the mean population size across the simulation time, considering only the simulations in which adult population size did not fall below the quasi-extinction threshold. In this case, we set the quasi-extinction threshold level to 30 marble trout, which is the minimum size observed for a viable pure marble trout population in the wild (Huda Grapa marble trout population, Fig. 1).

2.9. Sensitivity analysis

To assess the relative importance of model parameters on population viability, we implemented the sensitivity analysis approach proposed by McCarthy et al. (1995), as follows:

- (i) a set of model parameters was randomly sampled from the uniform distribution over the corresponding range of variation as reported in Table 2;
- (ii) 10 replicates of 100 years each were run by keeping the model parameters drawn at point (i) fixed for the entire simulation time ($t = 1 \dots 100$). As we performed the sensitivity analysis including both moderate and severe floods in the simulations (Scenario SF), the 10 replicates differed for the occurrence of the flood events;
- (iii) for each of the 10 replicates we computed two response variables: (a) the mean population size across the simulation time and (b) a binary variable set to 1 if the population dropped below the quasi-extinction threshold and 0 otherwise. The response variables were then associated to the corresponding model parameters drawn at point (i);
- (iv) we went back to point (i), randomly drew a new set of model parameters and replicated the process 1000 times;
- (v) we then explored the relationship between the 1000 values of model parameters (independent variables) drawn at point (i) and the 10,000 values of the mean population size and of the binary quasi-extinction variable (response variables).

Multiple ordinary regression with normal error structure was performed on the data set when the response variable was the mean population size. Logistic regression was used to explore the relationship between the probability of quasi-extinction (response variable) and the set of independent variables based on a logit transformation of a generalized linear model in the form

$$\text{logit}(p) = \ln\left(\frac{p}{1-p}\right) = \alpha_0 + \alpha_1 x_1 + \dots + \alpha_n x_n$$

where in this case p is the probability of extinction, x_n are the independent (predictor) variables and α_n are the regression coefficients.

The relative importance of each model parameter was indicated by its standardized regression coefficient, that is, the coefficient value divided by its standard error (Cross and Beissinger, 2001). The absolute value of the standardized regression coefficient represents the importance of the parameter in determining the future status of the population while the sign represents the direction of the contribution. To make the standardized regression coefficients comparable across the two streams we followed the approach of Zabel et al. (2006) and divided each standardized regression coefficient of each stream by the largest absolute value of the standardized regression coefficients for that stream. To assess the relative importance of the number of marble trout introduced in a fishless stream to create a new population, for each 10 replicates we also drew randomly the initial number of marble trout aged 1+ over a uniform distribution bounded between 100 and 1000.

3. Results

The mean population size estimated in the three scenarios and in the two streams were similar to those observed in Gorska and in Zakojska, respectively, during the sampling surveys between 1996 and 2004. Further simulations, not reported here, performed without density-dependence in first-year survival and by setting σ_0 equal to the mean of first-year survivals estimated from 1999 to 2004 produced unreasonable high abundances of marble trout in both Gorska and Zakojska, thus confirming the importance of density-dependence in first-year survival in the regulation of population abundance.

Population size exhibited remarkable variations over time under Scenario SF (including both severe and moderate flood events) as shown in the examples provided in Fig. 4, while for Scenario MF (only moderate flood events) and Scenario NF (no flood events) the variability in population size was less marked and abundance fluctuated around stream carrying capacity. Moreover, averages of mean population size across replicates were substantially lower with Scenario SF while quasi-extinction risk was clearly higher (Fig. 5).

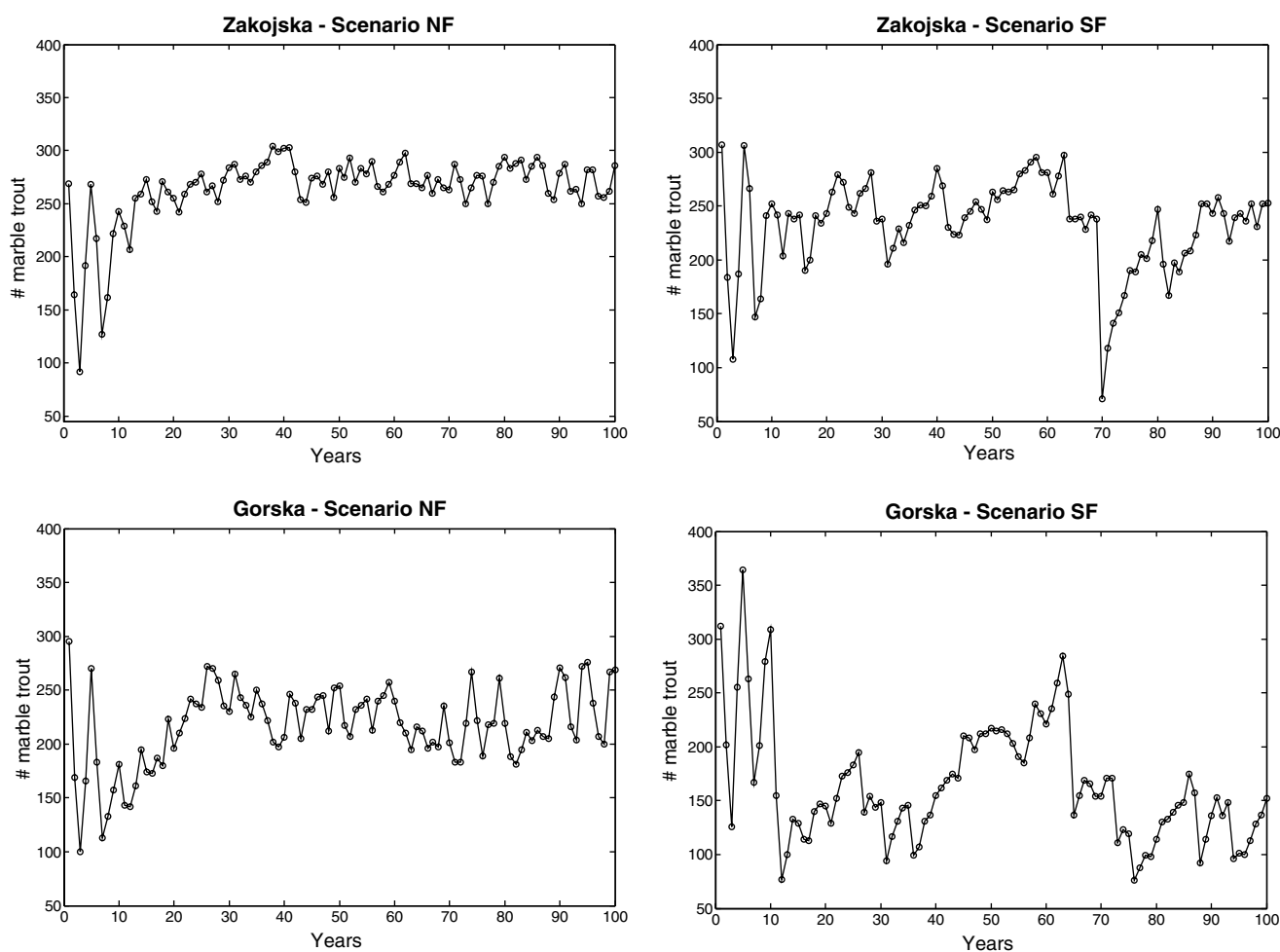


Fig. 4 – Examples of single simulations representing the time-varying number of marble trout in Scenario SF (both severe and moderate flood events) and Scenario NF (no flood events) for Gorska and Zakojska. As it can be noted from the examples provided, the modelling of both severe and moderate floods (Scenario SF) provides greater oscillations in the number of marble trout over the simulation time.

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. 5). The probability of dropping below 30 individuals was practically negligible under both the Scenario MF and Scenario NF while it was not trivial under the Scenario SF. Simulations showed that quasi-extinction risk was systematically larger in Gorska than in Zakojska (Fig. 5).

The sensitivity analysis showed that the demographic parameter that most affects both population size and quasi-extinction probability was γ (Table 3), that is the strength of density-dependence of first-year survival σ_0 (i.e., from egg production to 1+ year old trout). In fact, a larger γ implies a smaller first-year survival, a smaller recruitment of juvenile trout and, eventually, a smaller population size and a larger quasi-extinction probability. The importance of fecundity rates ($f_1..f_3$) and spawning probabilities ($sp_3..sp_5$) was marginal for both population size and quasi-extinction probability (Table 3), as the reproductive output (the actual number of eggs produced each year, which is obviously proportional to the fertility rates f_i) was modulated by the demographic

bottleneck provided by the density-dependent survival σ_0 . Survivals from age 1+ to sexual maturity had a considerable role, in particular when the response variable was the mean population size. The percentage reduction r_1 of population size due to severe floods greatly affected quasi-extinction probability but not population abundance, while the recurrence interval of floods (T_1 and T_2) played only a marginal role in affecting both the response variables (Table 3). Similarly, the initial number of marble trout introduced in the stream seemed to be not relevant, at least in the range of abundances of stocking material aged 1+ considered in the sensitivity analysis (Table 3). Other sensitivity analyses performed with quasi-extinction thresholds varying from 10 to 50 individuals showed similar results.

4. Discussion

One of the cornerstones of conservation biology is that small, fragmented populations should be considered locally vulnerable to extinction as they are strongly affected by highly variable climatic conditions and other environmental

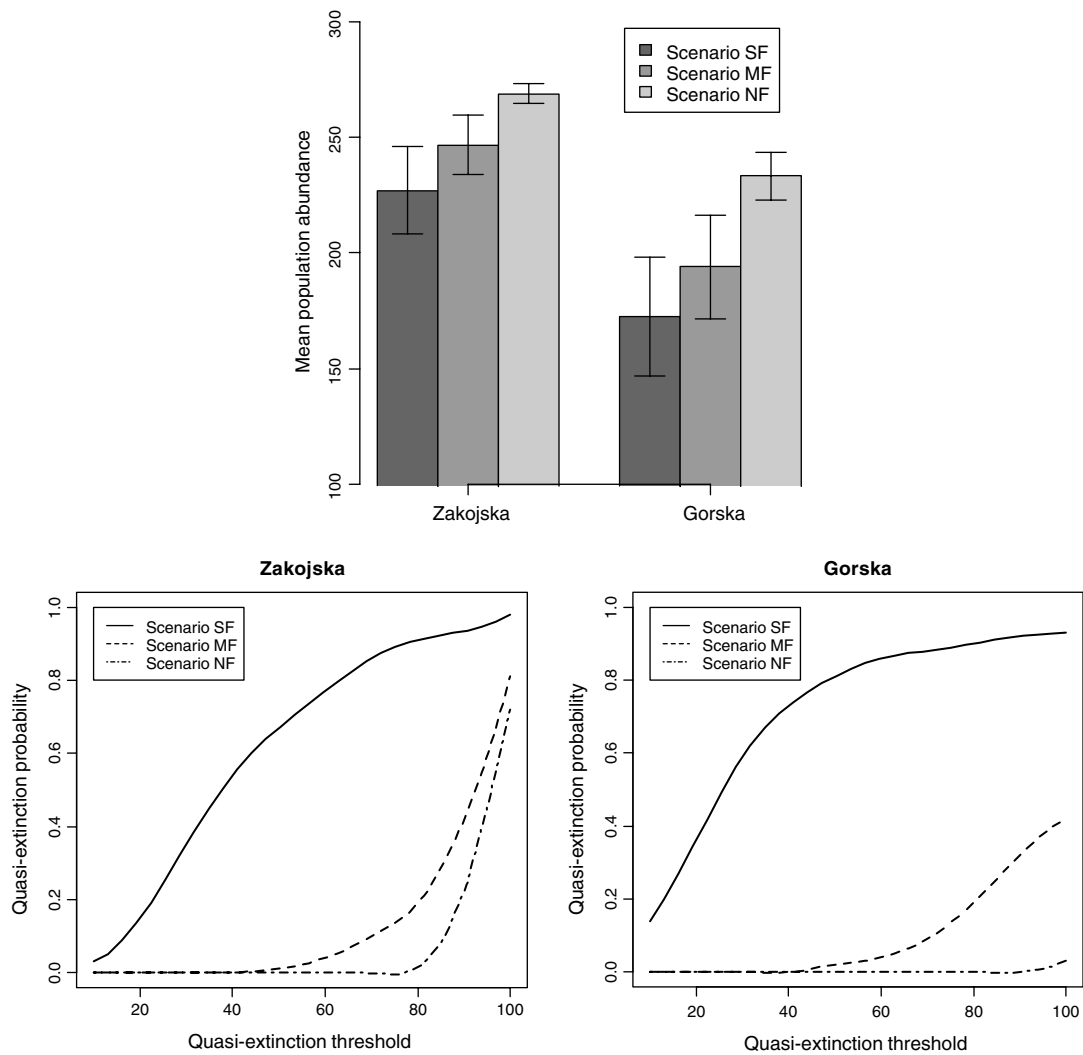


Fig. 5 – Results for mean population abundance \pm standard deviation and quasi-extinction probability from the stochastic model of marble trout population dynamics for Scenario SF (with both severe and moderate floods), Scenario MF (with only moderate floods) and Scenario NF (no floods).

and anthropogenic sources of disturbance that cause populations abundances to wildly fluctuate and possibly drop to very low densities. A large number of empirical observations, of field studies and of mathematical models to assess the risk of extinction of terrestrial and marine species have shown that the recovery of a small population to safe density levels may typically take a considerable amount of time or hardly occur because of inbreeding (e.g., Frankham, 1995), inverse density-dependence (Allee effect) (e.g., Boukal and Berec, 2002), altered sex ratio (e.g., Brown et al., 1994) and other demographic bottlenecks. The analysis we performed on marble trout populations living in pristine freshwater environments partially confirms this general picture. In the case of *S. marmoratus* living in Slovenian streams, major floods play a crucial role in determining population dynamics, also by considerably increasing the quasi-extinction risk (Fig. 5). Nevertheless, even by considering both the occurrence of severe and moderate floods (Scenario SF), the probability of dropping below 30 individuals (the mean size of the smallest viable marble trout population in the study

area, Huda Grapa, Fig. 1) in 100 years (about 30 trout generations) is quite small (Fig. 5). Most importantly, major floods seem to be the only serious risk-factor for population viability of marble trout populations in these pristine environments. In fact, from the simulation analysis, the marble trout populations of Gorska and Zakojska proved to be quite stable in the absence of major flood events (Scenario MF and NF) and exhibited only moderate fluctuations around the stream carrying capacity (Fig. 4). Moreover, population recovery after a severe drop in population abundance caused by a major flood usually occurs in very few years (Fig. 4). This is possible because the reproductive potential of marble trout, that is its per-capita fertility rate, is very high compared to the streams carrying capacities, while first-year density-dependent survival – that usually acts as demographic bottleneck at high population densities – remarkably increases when eggs production decreases (Vincenzi et al., in press) as a consequence of the collapse of the parental stock after a major flood event. Therefore, even a small number of reproductive individuals that

Table 3 – Standardized regression coefficients estimated from the sensitivity analysis of the stochastic population viability analysis for marble trout populations living in Gorska and Zakojska

Model parameter	Mean abundance		Quasi-extinction probability	
	Zakojska	Gorska	Zakojska	Gorska
A	0.13	0.40	0.03	−0.35
γ	−1.00	−1.00	0.28	0.79
T_1	0.12	−0.06	−0.17	−0.16
T_2	−0.13	−0.09	0.06	0.15
r_1	0.00	0.05	1.00	1.00
r_2	−0.23	−0.21	0.14	0.28
n_0	0.01	0.02	0.02	0.00
σ_1	0.33	0.22	−0.13	−0.18
σ_2	0.26	0.23	−0.15	−0.08
σ_3	0.17	0.12	−0.07	−0.13
σ_4	0.04	0.03	−0.01	0.00
σ_5	0.00	0.00	0.00	0.00
f_3	0.12	0.22	−0.05	−0.11
f_4	0.15	0.17	−0.01	−0.13
f_5	0.03	0.00	0.02	−0.02
sp ₃	0.12	0.10	−0.02	−0.07
sp ₄	0.07	0.07	−0.04	0.02
sp ₅	0.10	0.15	−0.04	−0.12

survive severe floods is sufficient to successfully re-establish the pre-event population size in few years. Marble trout population living in this pristine environment thus exhibit demographic feedbacks that act as a buffer against potentially catastrophic events which greatly reduce population densities, such as major floods, and confer a considerable resilience to the population. The spike of 0+ observed in 2005 in Zakojska after the October 2004 flood highlights the resilience of marble trout to dramatic flood events. This conclusion is confirmed also by empirical observations, as seven small, viable, remnant (i.e., non-translocated) marble pure populations have been identified in other streams in the study area (Fig. 1). From the beginning of the Marble Trout Rehabilitation Project (1993) no long-lasting declining trend has been observed in these remnant marble trout pure populations; the only extinction (Predelica marble trout population, Fig. 1) was caused by a landslide in November 2000.

In summary, only extreme floods, landslides and probably also severe droughts, are able to trigger local extinction of marble trout populations in these pristine environments, otherwise marble trout is quite persistent and is able to quickly recover after severe flood events. Other salmonid species in freshwater habitat exhibited a considerable resilience to extreme flood events. Roghair et al. (2002) reported that a brook trout population living in the Staunton River (Virginia, US) quickly recovered after a catastrophic flood. The Gila trout population of McKnight Creek in the Gila River Drainage (New Mexico and Arizona, US) recovered in a few years to pre-event conditions after a catastrophic flood that caused a 90% drop of the population size (Propst and Stefferud, 1997). Another similar case was reported by Beaudou et al. (1995) for brown trout living in a Corsican river after a 40-year flood. The brown trout population almost entirely disappeared, but a few individuals which found shelter in less affected areas were sufficient to re-establish a normal size-structured population in a few years. The unstable nature of stream environments has

led to the assertion that stream fish populations may essentially be in a constant state of recovery from disturbance. Yet, if the habitat is still suitable after a major flood, abundance and density can quickly rebound to pre-event levels (Lamberti et al., 1991; Thorpe, 1994).

Stream and watershed features are obviously likely to affect population abundance and persistence. Gorska stream is characterized by high slope, high fragmentation of the stream bed and narrow walls. These morphological features are probably responsible for the high water flow in the stream after heavy rainfalls and might explain, along with the absence of flood plain in Gorska, why the population went extinct after the October 2004 flood. They may also explain while Gorska and Zakojska were fishless before the beginning of the rehabilitation project in 1996, while eight pure marble trout populations, experiencing the same climate drivers (i.e., rainfall patterns) of Gorska and Zakojska, have been viable for a long time in other streams in the same geographical area (Fig. 1). A detailed comparative analysis of the morphological and hydrological features of the watersheds and of the strength of the resulting water flow (especially in case of floods) in the streams still need to be performed to clarify this issue.

Our analysis has something to tell us also about translocation strategies. First, in pristine habitats it is likely that the number of trout stocked when creating a new population does not need to be as big as the number of marble trout translocated in 1996 in Gorska and Zakojska to create the new populations, that is 500 individuals. In fact, the sensitivity analysis performed in the present work showed that population viability is not remarkably affected by the abundance of stocking material as long as it ranges between 100 and 1000 individuals (Table 3). After an initial reduction of trout number (also due to adaptation to the new environment), trout that are able to reach sexual maturity will produce new viable cohorts and, then, in a few years compensatory (i.e., density-dependent) responses will regulate population size around the stream carrying capacity. Moreover, the species vital traits, in particular fecundity and spawning probabilities, seem to play a moderate role in determining mean population abundance and quasi-extinction risk (Table 3). Second, the careful examination of stream and watershed features of the site of translocation is highly recommended in order to avoid the selection of sites particularly sensitive to brief and violent alterations of the hydrological regime. In particular, careful attention has to be paid to the juvenile carrying capacity of the stream where the new population will be created, as the availability of suitable micro-habitat for juveniles seems to be the predominant limiting factor to mean population abundance and is also a major factor in determining the quasi-extinction risk (Table 3). As reported by Armstrong et al. (2003), the water velocity experienced by individual fish is the principle variable determining habitat suitability for juvenile salmonids.

Third, the selection of sites for rehabilitation should obviously avoid streams with poor water quality conditions or risk of hybridization. In fact, with the exception of catastrophic floods, hybridization with brown trout, water pollution and human induced habitat alteration seem to be the most

serious causes of concern for marble trout viability (Crivelli et al., 2000).

Fourth, the degree of fragmentation, and the length of stream between two impassable waterfalls, especially in one-way streams, should be carefully investigated before the translocation is implemented: the more fragmented and the shorter the sectors are, the higher will be the probability of quasi-extinction.

Obviously, other factors have to be considered when creating new populations in fishless streams (Berg and Jørgensen, 1991), such as economic constraints, time and place of release, quality and age of the stocking material, etc. (Deverill et al., 1999). Further studies will be needed to investigate the ability of marble trout to colonize pristine environment, to identify other compensatory responses that can influence population dynamics such as density-dependent growth (Jenkins et al., 1999; Imre et al., 2005) and to quantitatively define the relationship between the strength of the stream water flow during a flood event and the consequent reduction in population size and alteration of spawning grounds. Another field of investigation is the analysis of the genetic risk associated with strong reductions in population size after flood events and with a low stocking material size. However, as reported by Fumagalli et al. (2002) the low genetic variability of the remnant marble trout populations living in pristine Slovenian streams ($H_0 = 0.04$ for the marble trout population of Huda Grapa) does not seem to affect the viability of these populations.

Despite these caveats, we are confident that implementing population viability analysis is useful to increase the success of rehabilitation projects of stream-living salmonid species. Population viability analysis remains one of the best available modelling approaches to evaluate management options for sensitive or threatened populations for which only scant data is available, as it allows us to explicitly include uncertainty in parameter estimation (Sarrazin and Barbault, 1996; Meffe and Carroll, 1997; Sutherland, 1998). Even decades of data may not be sufficient to reduce the uncertainty in crucial model parameters (Ludwig, 1999), such as, in our case the recurrence interval of flood events and the consequent reduction in population size, but the results of simulation analyses are still valuable when interpreted relative to other scenarios (Lindenmayer and Possingham, 1996), as it has been done in the present study. Modelling results are especially useful if the demographic details underlying the population dynamics have been obtained by systematic analysis on data gathered from well-tuned, long-term monitoring programs of existing populations. Although the identification of key vital traits or exogenous events does not automatically confer management significance to these factors, the modelling exercise developed in the present study is still useful to explore the population dynamics of marble trout populations living in Slovenian streams, to identify potential threats to their survival and to provide basic information to guide translocation and management of marble trout populations. We thus believe that the results here presented may be a valuable tool for conservation managers to prioritize the conservation actions necessary in order to enhance the viability of marble trout *S. marmoratus* in the Adriatic basin of Slovenia.

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