Eco-evolutionary dynamics induced by massive mortality events

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An eco-genetic model tuned on a population of marble trout *Salmo marmoratus* subject to periodic flood events was used to explore how the evolution of growth rates interacting with density-dependent processes can modify size at age and population structure and in turn influence the resilience of populations. Fish with greater growth potential were assumed to have higher mortality rates. The results of simulations were compared between two scenarios, one in which populations may evolve growth rates and the other one in which the distribution of growth rates within a population is kept fixed. Evolving populations had a greater proportion of age 1 year individuals in the population, greater median length at age 3 years (the typical age at sexual maturity for *S. marmoratus*) and lower population sizes. The slightly smaller population sizes did not affect realized extinction risk. Resilience, defined as the number of years necessary to rebound from flood-induced population collapse, was on average from 2 to 3 years in both scenarios, with no significant difference between them. Moderate heritability of growth, relaxation of density-dependent processes at low densities and rapid recovery to a safe population size combine to limit the capacity to evolve faster recovery after flood-induced population collapses *via* changing growth rates.

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INTRODUCTION

Life-history traits, such as body size and growth rates, fecundity, maturation schedules and iteroparity or semelparity, are important contributors to population dynamics. Also, they largely determine the extent to which populations can persist in the face of catastrophic disturbances (*i.e.* sudden and unusually severe reductions in population size; Mangel & Tier, 1993) and how quickly they can recover from them. For instance, opportunistic life histories in fish species are predicted to increase the probability of a population persisting after a collapse, as low generation times and high reproductive

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effort in general yield higher intrinsic rates of population increase than longer genera-
tion times and a lower annual reproductive effort (Winemiller, 2005). The ability of a
population to persist in the face of severe disturbances has often been considered as a
measure of stability, which can be further differentiated into resilience and resistance.
Resilience of a population [analogous with Holling's (1996) 'engineering resilience']
is the degree to which population is able to recover from disturbance without major
persistent changes in structure, as well as the time to return to equilibrium or steady
state in population size, age and size structure (Gunderson, 2000). On the other hand,
resistance is often defined as the amount of disturbance a system can absorb without
undergoing a fundamental change (Grimm & Wissel, 1997).

   The focus of this work is resilience of populations, which is the ability of a population
to recover after a catastrophic disturbance, as well as the eco-evolutionary dynam-
ics associated with catastrophic disturbances. Eco-evolutionary dynamics have been
widely investigated in recent years (Ghalambor *et al.*, 2007; Einum *et al.*, 2008; Kin-
nison *et al.*, 2008, 2011; Coulson *et al.*, 2010; Waples *et al.*, 2010; Carlson *et al.*, 2011)
and may be broadly defined as reciprocal, and possibly cyclical, interaction between
ecology and evolution, where ecological factors (*e.g.* density dependence) drive or cre-
ate the conditions for evolutionary change in phenotypes that in turn alter ecological
interactions (Post & Palkovacs, 2009).

   For fishes, the interplay between population collapses, recoveries and life histories
has been mostly studied in marine systems (Hutchings & Reynolds, 2004; Perry *et al.*,
2010; Hidalgo *et al.*, 2011), in particular in the context of fishing-induced evolution of
life histories (Ernande *et al.*, 2004; Enberg *et al.*, 2009, 2012). Predicting the rebuild-
ing of a depleted stock requires a good understanding of the factors that influence both
recovery dynamics and the associated time scales. Changes in harvested populations
(*i.e.* life span of fishes, population growth rate, life histories like age at sexual matura-
tion, egg production and egg size) can substantially modify the resistance and resilience
of fish populations to climatic fluctuations and the additional exploitation of the stock
(Hutchings & Reynolds, 2004; Walsh *et al.*, 2006; Perry *et al.*, 2010; Planque *et al.*,
2010).

   Results from simulation analyses showed that fisheries-induced evolution might not
always have easily predictable consequences on recovery rates. Kuparinen & Hutch-
ings (2012) simulated the demographic and evolutionary dynamics of a Atlantic cod
Gadus Morhua L. 1758 population subject to a 100 year period of size-selective har-
vesting, then followed by a 300 year recovery period with no harvesting. They sim-
ulated the demographic and evolutionary dynamics either by allowing life histories
to evolve during and after the fishing period or by assuming that fisheries-induced
evolution was absent. They found that despite the evolution of different life histories
between the evolutionary and non-evolutionary simulations, recovery rates were not
different between the two scenarios. Their conclusion was that in the absence of fish-
ing, the fitness (*i.e.* cumulative reproductive output) of the different life histories was
very similar.

   The present work focuses on unselective catastrophic disturbances, *i.e.* distur-
bances that induce massive mortalities, but due to their effect and rarity, there are
no phenotypes in the population having more chances to survive the disturbance
than others. Hurricanes, floods, oil spills, hypoxic events, harmful algal blooms and
coral bleaching are examples of disturbances with massive, but largely unselective,
consequences. The strong reduction in population size following the event, however,

creates new habitat and population conditions (*e.g.* low density) that may confer higher fitness to faster life histories.

Faster life histories following a catastrophic disturbance may arise through phenotypic plasticity or natural selection, which in turn may affect population-level traits like age-structure through eco-evolutionary dynamics and feedbacks (Post & Palkovacs, 2009; Waples *et al.*, 2010; Carlson *et al.*, 2011). Rapid growth is often favoured when there are time constraints for reaching a minimum size, an opportunistic strategy usually found under high disturbance (Arendt, 1997), and it may increase fitness in populations going through boom-and-bust cycles, such as populations periodically affected by flood-induced high mortalities. Rapid growth often comes at a cost, usually in the form of higher risk of mortality (Arendt, 1997; Billerbeck *et al.*, 2001; Lankford *et al.*, 2001; Enberg *et al.*, 2012).

Freshwater salmonids are an ideal model system for investigating the eco-evolutionary effects of unselective catastrophic disturbances, as severe and unpredictable extreme flow events such as flash floods and debris flows (*i.e.* when there is extensive erosion on steep, debris-mantled slopes) often induce massive mortalities without selecting directly for particular phenotypes. Extreme flows can be classified as extreme climatic events, as extremity is coupled climatically and ecologically (Smith, 2011). When the habitat after a catastrophic event is still suitable, abundance and density can quickly rebound to pre-event levels or beyond in just a few years (Lamberti *et al.*, 1991; Thorpe, 1994). Some studies have shown that adult and juvenile salmonids displaced downstream by floods have returned upstream after the flood recedes; also, recolonization by unaffected sub-populations living nearby can be quick (Dedual & Jowett, 1999; Ortlepp & Murle, 2003).

If the population has not been completely extirpated, a few survivors can rapidly increase population size to pre-event population levels due to intrinsic processes. Vincenzi *et al.* (2008*a*) used a simulation analysis to conclude that relaxation of density-dependent pressure at low densities may increase the resilience of salmonid populations to catastrophic floods through an increase in growth. Since body size is positively related to the number of eggs produced by a female, low densities following episodes of massive mortalities allow for an increase in growth rates (Elwood & Waters, 1969; Jenkins *et al.*, 1999; Roghair *et al.*, 2002) that carry over to an increased reproductive output in the years immediately following the extreme event. In addition, Vincenzi *et al.* (2012*a*) showed that in stream-dwelling marble trout *Salmo marmoratus* Cuvier 1829, massive mortalities caused by extreme flows can substantially reduce variability in growth rates (*i.e.* coefficient K of the von Bertalanffy growth model) with respect to populations not subject to periodic heavy losses.

Variation in timing, predictability, frequency and severity of catastrophic flood events makes it difficult to predict the contribution of the evolution of a trait-like growth to the resilience of populations. To do so, it is necessary to couple trait dynamics with individual dynamics (Björklund *et al.*, 2009; Vincenzi *et al.*, 2012*b*). For example, while rapid growth may be advantageous under high disturbance, in the presence of a trade-off between growth and survival populations may be trapped at low densities (Botsford, 1981), thus increasing the risk of extinction following subsequent massive mortality events. In addition, the substantial variations in population density often observed in stream-dwelling populations, even in the absence of catastrophic events, and the well-described density dependence of growth and size at age, make it particularly challenging to observe intrinsic differences in growth rates across years

as well as to tease apart the relative contribution of density and intrinsic growth rates on the realized growth of individuals. As density-dependent processes are also likely to shape life histories (Engen *et al.*, 2005; Bonenfant *et al.*, 2009), it is important to capture those processes.

In this work, an eco-genetic model (Dunlop *et al.*, 2009) was used to explore how the evolution of growth rates in a salmonid population subject to catastrophic events and its interplay with density-dependent processes can modify size at age, population structure and in turn influence the resilience of populations to catastrophic flood events. Model parameters were tuned on data from a population of *S. marmoratus* living in a Slovenian stream, for which autumnal flash floods and debris flows are a major threat to viability (Vincenzi *et al.*, 2008*a*, *b*, 2010, 2012*a*).

MATERIALS AND METHODS

MODEL SYSTEM

Salmo marmoratus is a stream-dwelling salmonid endemic to the Po River basin of Italy and Adriatic basin of Slovenia with non-hybrid populations currently restricted to secluded head-water streams in northern Italy and Slovenia, although *S. marmoratus* haplotypes have been found in Switzerland, the Adriatic basin of Italy and Albania (Crivelli *et al.*, 2000). Ten populations of *S. marmoratus* have been monitored in Slovenia within the Soca, Idrijca and Baca River basins by annual or bi-annual sampling starting from 1996 within a conservation project for the genetic rehabilitation and conservation of the species (Crivelli *et al.*, 2000; Vincenzi *et al.*, 2012*c*). *Salmo marmoratus* show a high plasticity in body size; hybrid fish 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 mass and total length (L_T) were 650 g and 400 mm. In the monitored streams, the maximum observed age was 10 years, but very few individuals were older than 6 years. *Salmo marmoratus* feed generally on bottom-dwelling organisms and on aquatic invertebrates. Cannibalism by adults on juveniles has been observed, although the extent of cannibalism and conditions leading to it are still not clear and deserve further investigation. Spawning takes place in November to December, eggs hatch generally in March, with emergence occurring in May to June. Data from fish farm and from natural populations show evidence of iteroparity (Meldgaard *et al.*, 2007).

FLOODS IN THE STUDY AREA

The dramatic effect of severe flood events on *S. marmoratus* populations became evident in October 2004, when flash floods and debris flows occurred in several streams within the Soca, Idrijca and Baca River basins and caused a substantial reduction in population size in all monitored populations. The reductions in population size ranged from 31 to 78%, but most of the populations quickly recovered to pre-event numbers (Vincenzi *et al.*, 2012*c*). Such catastrophic events have a presumed recurrence interval of 50–100 years, but their frequency appears to be increasing (Vincenzi *et al.*, 2012*c*). Flash floods in November 2007 and 2009 caused a drastic reduction in population size in several populations, with the populations of Zakojska and Lipovesck reduced to < 10 individuals each and still facing a high risk of extinction, although a large number of age 1 and 0 year fish were sampled 2–3 years after the floods (A. J. Crivelli, unpubl. data).

MODEL OF POPULATION DYNAMICS

The eco-genetic model used here is an extension of the model of population dynamics of *S. marmoratus* by Vincenzi *et al.* (2012*a*) (Fig. 1). The model is used to explore how the distribution of individual growth rates in a population of the stream-dwelling salmonid evolves with the occurrence of flood events and whether the evolution of growth rates contributes to
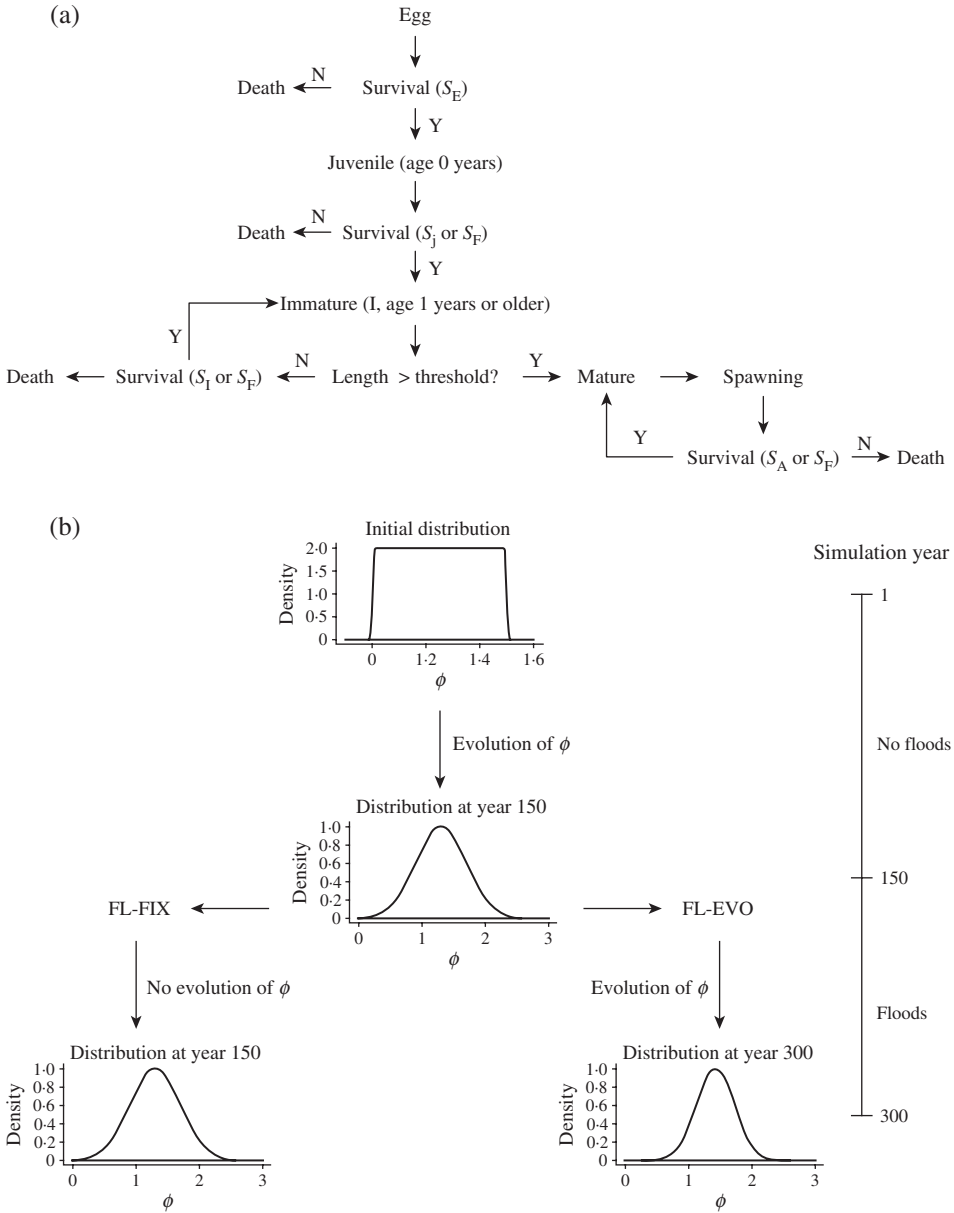
(a)

Egg
↓
Death ←—N— Survival (S_E)
↓ Y
Juvenile (age 0 years)
↓
Death ←—N— Survival (S_j or S_F)
↓ Y
→ Immature (I, age 1 years or older)
↓
Y |
Death ←— Survival (S_I or S_F) ←—N— Length > threshold? —Y→ Mature —→ Spawning
↓
Y |
Survival (S_A or S_F) —N→ Death

(b)

Initial distribution

Distribution at year 150

FL-FIX ←

No evolution of ϕ

Distribution at year 150

Evolution of ϕ

→ FL-EVO

Evolution of ϕ

Distribution at year 300

Simulation year

1

No floods

150

Floods

300

FIG. 1. (a) Schematic representation of the model of population dynamics for *Salmo marmoratus*. (b) Evolution of growth rates in the scenarios FL-FIX and FL-EVO. Growth rates evolve in the first 150 years in the absence of flood events in both scenarios. Then, flood events were introduced for the next 150 years. In scenario FL-EVO, offspring inherit growth parameter (ϕ). In scenario FL-FIX, at each time step, each offspring draws a growth parameter randomly from the normal distribution fitted on the pooled distribution of growth potentials in the last 5 years before the introduction of floods. For the scenario FL-FIX, at year 300, the distribution of ϕ is the same as the one at year 150. S_j, survival of juveniles; S_I, survival of immature fish; S_A, survival of adults; S_F, survival probability in the case of flood event.

population persistence as well as population-level traits like population size, age and size structure. In this model, a common baseline is established by allowing simulated populations of *S. marmoratus* to evolve in a fluctuating environment without floods and to reach a quasi-stable distribution in population-level traits (age and size structure, population size and growth rates). Then, extreme rainfall that may induce flash floods and debris flows causing sudden and massive mortality is added to the simulations (FL). Floods affect the population before spawning (Vincenzi *et al.*, 2012*c*. The distribution of growth rates can evolve (FL-EVO) or remain fixed (FL-FIX) during this subsequent simulation period (Fig. 1). Only females were modelled. Each fish is characterized by a multiplier of growth ϕ (growth potential) that affects both its survival and growth. Individuals in their first year of life (from zero to one winter) are referred to as juveniles, and fish older than age 1 year but not reproductively active as immature. After sexual maturity, fish are defined as adults. The model was parameterized with reference to the *S. marmoratus* population of Zakojska (Slovenia; Vincenzi *et al.*, 2008*b*, 2012*c*).

GROWTH

In *S. marmoratus*, density conditions experienced during the first year of life have a long-lasting influence on the growth of the fish (Vincenzi *et al.*, 2008*c*), and the same process has also been observed in brook trout *Salvelinus fontinalis* (Mitchill 1814) (Letcher *et al.*, 2011). Length at age is modelled as von Bertalanffy growth with asymptotic size set by density experienced in the first year of life [Fig. 2(a)]. Thus, for an individual of age a, Brody's growth rate K, theoretical age at which length is 0 a_o, density of *S. marmoratus* $\geq$ age 1 year during its first year of life (density as underyearling, D_U, individuals m^{-2}), asymptotic length when D_U approaches 0 L_∞, growth potential ϕ, expression parameter ϵ and strength of density dependence γ and Length at age is:

$$L\left(a|D_U,\gamma,\phi,\epsilon\right) = L_\infty \left(1 + \gamma\, D_U\right)^{-1} \left(1 - e^{-K\phi\epsilon(a-a_o)}\right) \tag{1}$$

Parameter names and values are summarized in Table I. Model parameters were estimated by non-linear least-squares regression using data in Vincenzi *et al.* (2008*a*, *b*). For simplicity,
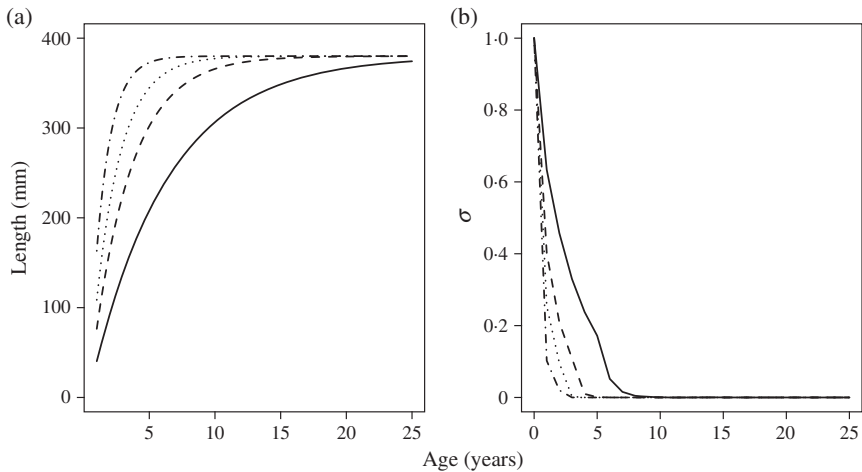

FIG. 2. (a) Growth trajectories and (b) survival curves for *Salmo marmoratus* with growth potential ϕ 0·5 (——), 1 (— — —), 1·5 (.......) and 2·5 (. — . —). The density of fish $\geq$ age 1 year in the first growth period D_u, the density of juveniles D_j and the density of fish $\geq$ age 1 D_A were set to 0·5. Survival to age zero was normalized to 1.

TABLE I. Variables and parameter values for the model of *Salmo marmoratus* population dynamics

Model	Parameter or variable	Estimates	Source
	Parent P_M	–	–
	Offspring O	–	–
	Growth potential ϕ	–	–
	Mortality rate in case of flood event M_F	–	–
	Annual survival for adults S_A	–	–
	Annual survival of immature fish S_I	–	–
	Survival of juveniles S_j	–	–
	Survival probability in case of flood events S_F	–	–
	Eggs E	–	–
	Density of fish $\geq$ age 1 year in the first growth period D_u	–	–
	Density of juveniles D_j	–	–
	Density of fish $\geq$ age 1 years D_A	–	–
	Gene expression parameter ϵ	–	–
	Age A	–	–
Density-dependent growth	Strength of density-dependent growth γ	0·1	Data from Vincenzi *et al.* (2012*a*)
	Asymptotic length in the vB model L_∞	380	
	Brody's growth rate in the vB model K	0·34	
	Theoretical age at which length is 0 in the vB model a_0	0·34	
Reproduction	s.d. of the normal distribution for transmission of growth potential from parent to offspring σ_τ	0·1	Vincenzi *et al.* (2008*b*, 2012*a*)
	Terms describing length-dependent egg production α_E	−750	
	β_E	3·8	
Mortality	Mortality as densities approach 0 M	0·48	Data from Vincenzi *et al.* (2012*a*) and S. Vincenzi & A. J. Crivelli, unpubl. data
	Strength of density-dependent mortality for juveniles ω_j	3	
	Strength of density-dependent mortality for immature fish ω_I	1·2	

TABLE I. Continued

Model	Parameter or variable		Estimates	Source
	Cost (increased mortality) of reproduction	ν	2	
	s.d. of gene expression parameter	σ_ϵ	0·3	
Floods	Mean and s.d. on the arithmetic scale of the distribution of rainfall	μ_F	298	Data from Vincenzi *et al.*
		σ_F	327	(2008a)
	Terms describing flood-dependent mortality	α_F	1·7	
		β_F	0·0018	
	Maximum mortality rate in case of flood	M_{max}	2·8	

density at later years was not considered in the model of growth, as it seems to have only a minor role in determining growth trajectories (Vincenzi *et al.*, 2007a). The growth parameter ϕ is a multiplier of growth rate K and is equal to $1-1\cdot5$ (with $\epsilon = 1$) for the population of *S. marmoratus* (base case) upon which the model parameters were tuned. The parameter ϵ represents stochasticity due to gene expression. In the model, L_∞ and γ were fixed population-level parameters, while ϕ and ϵ were individual-specific parameters.

REPRODUCTION

In salmonids, a positive relationship linking female length to sexual maturity and egg production is often observed (Jonsson & Jonsson, 2011). For *S. marmoratus*, the number of eggs produced E was related to body length L of female by the linear relationship:

$$E = \alpha_E + \beta_E L \tag{2}$$

where $\alpha_E < 0$, $\beta_E > 0$ and $\frac{|\alpha_E|}{\beta_E}$ is length at sexual maturation (Vincenzi *et al.*, 2007b) (Table I). Based on equation 2, length at maturity does not depend on growth rates, and thus age at maturity depends on both ϕ and density. Length at maturity is insensitive to variation in density in many fish populations, although the corresponding age at maturity can change substantially as a result of density dependence in growth (Mangel & Abrahams, 2001; Lorenzen, 2005). A number of studies on salmonid species have reported a general correlation between rapid growth and early sexual maturation (Hutchings & Jones, 1998; Utrilla & Lobon-Cervia, 1999), with slowly growing fishes delaying sexual maturation in order to reach the minimum size required for gonadal development.

Fish are assumed to spawn annually from maturity until death (Meldgaard *et al.*, 2007; A. J. Crivelli & D. Desensek, unpubl. data). In the wild, approximately one quarter to half of mature females reproduce successfully each year (Meldgaard *et al.*, 2007; A. J. Crivelli, unpubl. data). In the model, Bernoulli trials ($P_M = 0\cdot35$) were used to determine if eggs produced by each female each year are viable and thus included in the egg pool.

INHERITANCE OF GROWTH PARAMETER ϕ

The methodology of Dunlop *et al.* (2009) and Enberg *et al.* (2009) for eco-genetic models was used to model inheritance and expression of growth parameter, although there are some

differences between their approach and the one presented in this work both in the modelling of growth and the inclusion of either sex. Stochasticity was introduced in the correlation between genotypes and phenotypes to broadly represent different processes as: (1) inheritance of trait and (2) phenotypic expression of trait.

Two parameters were thus introduced: (1) τ, which is added to ϕ and represents stochasticity due to mutation–segregation–recombination processes. The value of τ is randomly drawn from $N(0, \sigma_\tau)$ (Table I). The growth parameter of the offspring ϕ_o depends on the growth parameter of the parent (female) ϕ_p and the parameter τ;

$$\phi_O = \phi_p + \tau \tag{3}$$

and (2) ϵ, which represents stochasticity due to gene expression (equation 1). ϵ is derived once from $N(1, \sigma_\epsilon)$ for each individual and kept for its entire life.

The parameter σ_ϵ was chosen following a pattern-oriented modelling strategy (Grimm $et\ al.$, 2005). Simulations were performed using the model of population dynamics by varying σ_ϵ and looking for values of heritability h^2 of body size at age 1 year in the range $0\cdot2–0\cdot4$ (Funk $et\ al.$, 2005; Carlson & Seamons, 2008). As only one sex was modelled, selected values for the parameter σ_ϵ were those leading to the slope of parent–offspring relationship of $0\cdot1–0\cdot2$ ($i.e.$ half of the h^2 when mid-parent values are considered) (Falconer & Mackay, 1996).

SURVIVAL

Egg to age 0 year survival (S_E) was assumed to be density independent and constant across ϕ in the absence of floods. For older life stages, survival probabilities are specific for each individual, as they depend on ϕ and ϵ, as described below.

Juvenile (from age 0 year to one winter) survival S_j was density dependent:

$$S_j \left(M, \omega_j, D_j, \phi \right) = e^{-M\left(1 + \omega_j D_j\right)\phi\epsilon} \tag{4}$$

where M is the annual mortality when densities approach zero, D_j is the density of juveniles (individuals m^{-2}) and ω_j describes the strength of density dependence for juvenile survival (Vincenzi $et\ al.$, 2007b, 2008a). Vincenzi $et\ al.$ (2008a) did not find any evidence for size-selective mortality in $S.\ marmoratus$ so that S_j is independent of size.

The growth-mortality trade-off for the individual is determined by the growth parameter ϕ and the expression parameter ϵ [Fig. 2(b)]. As $S.\ marmoratus$ have no predators in the mountain streams where they live, growth-mortality trade-off should be considered as emerging from reduced allocation of resources to other functions ($e.g.$ maintenance, repair and development of the immune system) when growth rates are maximal. For simplicity, and in absence of empirically validated models for $S.\ marmoratus$, a multiplicative effect of $\phi\epsilon$ on instantaneous mortality rate was assumed.

Annual survival S_I for sexually immature fish was:

$$S_I \left(M, \omega_A, D_A, \phi, v \right) = e^{-M\left(1 + \omega_A D_A\right)\phi\epsilon} \tag{5}$$

where D_A is the population density of fish > age 1 year (individuals m^{-2}) and ω_A characterizes the strength of density dependence for survival. Parameters of equation (5) were estimated from mark-recapture data (Vincenzi $et\ al.$, 2012c).

For sexually mature fish, equation (5) was modified to account for spawning mortality:

$$S_A \left(M, \omega_A, D_A, \phi, v \right) = e^{-M\left(1 + \omega_A D_A\right)\phi\epsilon v} \tag{6}$$

where ν characterizes the cost of reproduction. The value of ν was obtained from experiments performed in a fish farm (S. Vincenzi & A. J. Crivelli, unpubl. data) [Fig. 2(b)].

Survival probability S_F in case of flood events, applied equally juveniles, immature and adult fish, was modelled as:

$$S_F = e^{-M_F(R)} \tag{7}$$

where $M_F(R)$ is the mortality induced by the flood event, depending on monthly rainfall R. In case of $R > 400$ mm (Vincenzi *et al.*, 2008*a*), mortality is assumed to be independent of growth parameter ϕ, density and age, and thus S_F substitutes for the respective age-class. The relationship was developed between the intensity of a flood event and mortality M_F using empirical data and expert knowledge, with autumnal rainfall recorded in the study area used as a proxy for flood event. For $R > 400$ mm:

$$M_F(R) = \min\left(\alpha_F + \beta_F R, M_{\max}\right) \tag{8}$$

where R was monthly rainfall in November (mm). Rainfall > 1000 mm (for which $M_F(R) = M_{\max}$) has a recurrence time of *c.* 20 years. Floods were assumed to be unpredictable and thus to have no selective consequences on timing of spawning, morphology or behaviour of fish.

SIMULATION SCENARIOS

The model was run for 250 replicates for each scenario. Each simulation was started with 300 age 1 year individuals, each individual having a randomly assigned growth parameter ϕ from a uniform distribution bounded between 1 and 1·5 and a length defined as in equation (1) for $a = 1$. In all scenarios, (1) demographic stochasticity was implicitly included and (2) environmental stochasticity was modelled by randomly drawing values of model parameters at each time step (common to all fish for that time step) of the simulation from the uniform distribution [0·95 P_M, 1·05 P_M], where P_M is the parameter value (Vincenzi *et al.*, 2012*a*).

In all scenarios, for each replicate, the simulation was run for 150 years with only stochasticity (*i.e.* no floods) and with inheritance of growth rates in order to obtain a quasi-stable distribution of growth rates at year 150 (ϕ_{150}). The appropriateness of 150 years as sufficient simulation time to obtain a quasi-stable population size, age and size structure was tested with preliminary simulations. In particular, it was observed that from year 140 to year 150, the c.v. of the variables of interest was consistently and largely $< 0·2$.

For the remaining 150 years, catastrophic flows were modelled by randomly drawing at each time step (*i.e.* year) a value from the log-normal probability distribution fitted to autumn rainfall data recorded in the study area from 1961 to 2007 ($\mu_F = 300$ mm, $\sigma_F = 328$, both parameters are on the arithmetic scale) (Vincenzi *et al.*, 2008*b*). If monthly rainfall was > 400 mm, a catastrophic event occurred and survival of fish was modified.

Values of model parameters are provided in Table I. Densities were computed at each time step by dividing twice the number of individuals of the appropriate age class (assuming a 1:1 sex ratio, as only females were modelled) by stream surface area.

Floods affect the population before spawning (Vincenzi *et al.*, 2012*c*). In the evolutionary scenario FL-EVO, offspring then inherit growth parameters, while in scenario FL-FIX, at each time step, each offspring draws a growth parameter randomly from the normal distribution fitted on the pooled distribution of growth potentials in the last 5 years before the introduction of floods. Re-sampling from the empirical pooled distribution of growth potentials in the last 5 years before the introduction of floods did not change model results.

Although flash floods and debris flows can substantially modify stream habitat (alterations of biotic communities and physical structure of streams, creation or loss of habitat), their consequences are largely unpredictable. In some cases, in-stream habitat can improve, as the coarsening of the substratum may provide better habitats for fishes (Jenkins, 1969; Bjornn, 1971; Moyle & Marchetti, 2006). In other cases, spawning grounds can be severely reduced in size or the gravel made unstable, and pools and riffles filled with sands and debris. Accordingly, the surface area of the stream was assumed to be constant over time and equal to 900 m^2, and

random variation in vital rates incorporated the effects of floods on habitat. Population size and distribution of individual growth rates were computed in the autumn, before spawning and after the potential occurrence of floods. At each time step, Bernoulli trials defined survival of each individual. In the model, eggs were spawned in the autumn and age 0 year fish emerged in the following year in late spring to early summer.

Each simulation lasted 300 years (*i.e.* finished 150 years after reaching the quasi-stable distribution) and persistence or quasi-extinction of the population was recorded. The quasi-extinction thresholds q_t used ranged from one to 20 fish present in the population. If a population went below q_t at any time during the simulation, the population was considered quasi-extinct.

When analysing model results as reported below, populations with no females older than age 0 years were considered as extinct, and further analyses were carried out only for populations that persisted up to the end of simulation time. For each replicate of each scenario, the median population size in the last 50 years of the simulation and the mean, maximum and range of the final distribution of ϕ (ϕ_{300}) were computed, and the means of the descriptors of growth potential in the populations and population size were compared using t-tests. In order to test for faster life histories with the evolution of growth rates, proportion of age 1 year individuals in the populations, prop(age-1), was computed in either scenario (FL-EVO and FL-FIX), and linear regression models were fitted for both the FL-EVO and FL-FIX scenarios for prop(age-1) on simulation year t in the form $\mathrm{prop}(\mathrm{age}-1)_{\mathrm{tend}} = \alpha_{\mathrm{prop,tend}} + \beta_{\mathrm{prop,tend}}t$, where a positive slope parameter β_{prop} describes an increase in proportion of age 1 year fish through time. A sample of time series was visually checked for serious violations of assumptions of the linear model. Subsequently, a t-test was used to test for significant differences in mean β_{prop} between the two scenarios. Both significant and non-significant (at the 0·05 level) β_{prop} were used for the t-test. In addition, a t-test was used to test for differences in median prop(age-1) in the last 50 years of simulation time (*i.e.* from year 250 to 300) between scenarios.

In order to test whether the evolution of growth rates and their interplay with density led to increased realized size at age, linear regression models were fitted for both the FL-EVO and FL-FIX scenarios for median size at age 3 years at year t, $\widetilde{L}_{3,t}$ (*i.e.* the typical age at sexual maturity, from now on the subscript t is skipped to simplify notation) on simulation year t in the form $\widetilde{L}_{3,\mathrm{tend}} = \alpha_{L,\mathrm{tend}} + \beta_{L,\mathrm{tend}}t$. The time series upon which the models were developed start for each replicate at year 150 and end at year t_{end}. $t_{\mathrm{end}} = 200$ and $t_{\mathrm{end}} = 300$ were used in order to account for the possibility that the introduction of floods may induce evolution toward a new quasi-steady state, but as this state is approached, evolution may slow down and a linear relationship may not be apparent over the course of the entire simulation. A positive slope parameter β_L describes an increase in median size of age-3 year ($\widetilde{L}_{3,\mathrm{tend}}$) fish through time. Also in this case, a sample of time series was visually checked for serious violations of assumptions of the linear model. A t-test was then used to test for significant differences in mean $\beta_{L,200}$ and $\beta_{L,300}$ between the two scenarios. Both significant and non-significant $\beta_{L,200}$ and $\beta_{L,300}$ were used for the t-test. In addition, a t-test was used to test for differences between scenarios in mean across replicates of mean $\widetilde{L}_3$ in the last 50 years of simulation time.

Resilience was defined as the number of years t_{f} necessary for populations to recovery to 50 individuals after being reduced below population size f (= 10 or 20 individuals). In order to avoid penalizing populations that by chance suffered additional massive mortalities within a few years, recoveries when another flood event occurred within 5 years of the previous event (not the entire replicate) were excluded from the analyses of resilience.

SENSITIVITY ANALYSIS

The robustness of model results to alternative assumptions regarding the shape of the initial distribution of ϕ (uniform, beta and log normal) and the number of individuals (ranging from 300 to 500) in the first year of the simulation was assessed. The interval of uniform distribution was widened to [0·9 P_{M}, 1·1 P_{M}] of estimates of model parameters (Table I) to test whether higher stochasticity changed simulation results. A more comprehensive sensitivity analysis can be found in Vincenzi *et al.* (2012*a*).

RESULTS

At the end of the 150 years without flood events, the simulated populations were similar to the Zakojska *S. marmoratus* population in terms of age and size structure and population size (empirical data from Zakojska, mean $\pm$ S.D. $\widetilde{L}_3 = 214 \cdot 35 \pm 24 \cdot 72$ mm, median number of females given a 1:1 ratio = 135). The simulated populations had *c.* 150 females at the end of the period with no flood events (Fig. 3) and $\widetilde{L}_3 = 213 \cdot 70 \pm 11 \cdot 60$ mm. Then, flood events were introduced and the populations periodically collapsed (Fig. 3), showing a spike of age 1 year fish one or two years following the catastrophic event due to the relaxation of density-dependent processes (Fig. 4). Fairly strong fluctuations of median body length of age 3 year fish $\widetilde{L}_3$ driven by the catastrophic floods were observed (Fig. 5). In the case of the scenario with evolving growth rates, $\widetilde{L}_3$ tended to increase linearly over time, while the same increase with the fixed growth rate scenario was not observed [Figs 5 and 6(b), (e)]. A *t*-test on β_L revealed a statistically significant large mean slope β_L for the FL-EVO scenario both at year 200 and year 300 (*t*-test, d.f. = 351·159 and d.f. = 437·346 for year 200 and 300, $P < 0 \cdot 01$ for both year 200 and year 300) and greater mean $\widetilde{L}_3$ in the last 50 years of the simulation (*t*-test, d.f. = 375·477, $P < 0 \cdot 01$, mean $\pm$ S.D. $\widetilde{L}_3$: FL-EVO = 232·8 $\pm$ 6·20 mm; FL-FIX = 213·70 $\pm$ 11·60 mm) [Fig. 7(a)]. In addition, $\beta_{L,200}$ was significantly greater than $\beta_{L,300}$ in scenario FL-EVO (*t*-test, d.f. = 199·34, $P < 0 \cdot 01$, mean $\pm$ S.D. $\overline{\beta}_{L,200} = 0 \cdot 18 \pm 0 \cdot 27$ mm year^{-1}; $\overline{\beta}_{L,300} = 0 \cdot 07 \pm 0 \cdot 07$ mm year^{-1}).

The proportion of young fish increased over time in the FL-EVO scenario, while it did not show an increase over time for the FL-FIX scenario [Figs 4 and 6(a), (d)]. A *t*-test on prop(age-1) found statistically significant larger mean slope β_{prop} for the FL-EVO scenario both at year 200 and year 300 (*t*-test, d.f. = 494·931 and d.f. = 472·091 for year 200 and 300, $P < 0 \cdot 01$ for both year 200 and year 300) and greater median prop(age-1) in the last 50 years of the simulation ($P < 0 \cdot 01$, mean $\pm$ S.D. of median prop(age-1): FL-EVO = 0·61 $\pm$ 0·02; FL-FIX = 0·54 $\pm$ 0·04) [Fig. 7(b)].

The median population size in the first 50 years after the introduction of floods and in the last 50 years of simulation time was larger for scenario FL-FIX (*t*-test, d.f. = 428·384 and d.f. = 461·516 for first and last 50 years, $P < 0 \cdot 01$ for both first and last 50 years, $\widetilde{\overline{N}} \pm$ S.D.: FL-EVO = 124·45 $\pm$ 17·69 and 114·23 $\pm$ 16·72 females for first and last 50 years; FL-FIX = 138·60 $\pm$ 11·77 and 130·73 $\pm$ 14·49 females) [Fig. 6(c), (f)]. The maximum ϕ at the end of simulation time was significantly greater in the FL-EVO scenario (*t*-test, d.f. = 452·346, $P < 0 \cdot 01$, mean $\pm$ S.D. of maximum ϕ: FL-EVO = 2·63 $\pm$ 0·19; FL-FIX = 2·55 $\pm$ 0·24) as well as the minimum ϕ (*t*-test, d.f. = 457·505, $P < 0 \cdot 01$, mean $\pm$ S.D. of minimum ϕ FL-EVO = 0·92 $\pm$ 0·19; FL-FIX = 0·57 $\pm$ 0·24), while range of ϕ was significantly greater in the FL-FIX scenario (*t*-test, d.f. = 444·521, $P < 0 \cdot 01$, mean $\pm$ S.D. of range of ϕ: FL-EVO = 1·71 $\pm$ 0·28; FL-FIX = 1·97 $\pm$ 0·37) (Fig. 8).

The risk of quasi-extinction was similar for both scenarios across quasi-extinction thresholds ranging from one to 20 females (Fig. 9). Resilience from relatively less severe reductions in population size following flood events (*i.e.* time to rebound to 50 individuals after collapsing below 20 fish, t_{20}) was not different between scenarios (Mann–Whitney *U*-test, W = 280056, $P > 0 \cdot 05$) with mean $\pm$ S.D. $\overline{t}_{20} = 2 \cdot 07 \pm 0 \cdot 36$ and $2 \cdot 07 \pm 0 \cdot 33$ years for FL-EVO and FL-FIX. Resilience from the most severe flood events (rebound from collapsing below 10 fish, t_{10}) was not significantly different
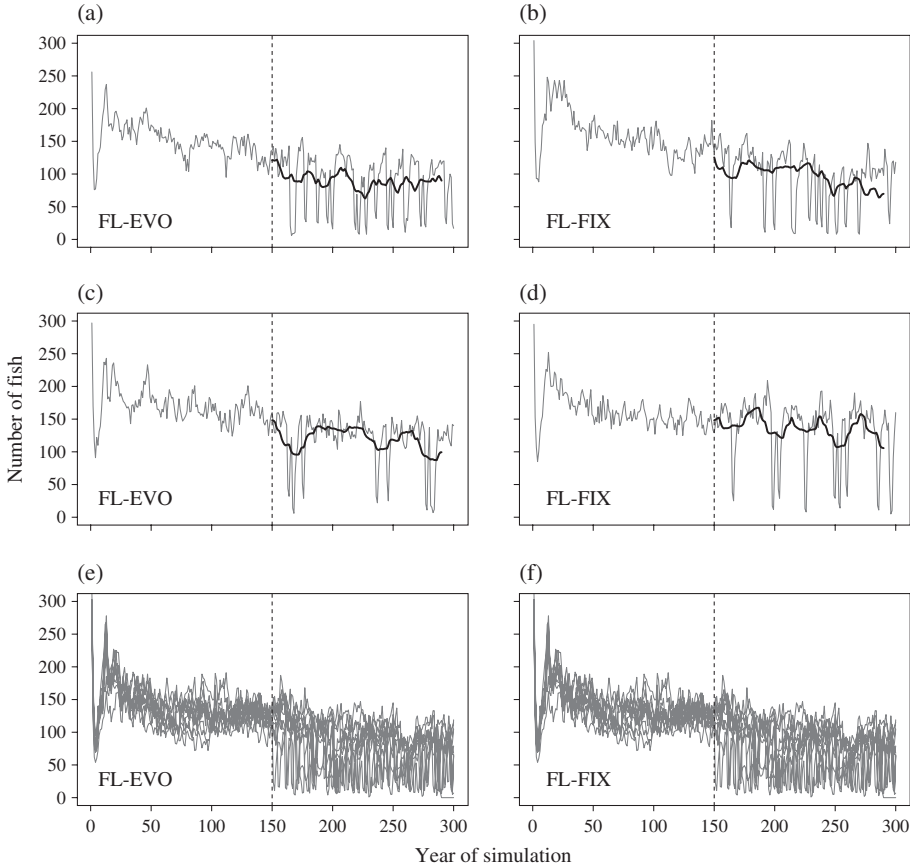
FIG. 3. Examples of individual trajectories with 10 year moving averages (———) for the scenarios (a) and (c) with evolution of *Salmo marmoratus* growth rates (FL-EVO), and (b) and (d) with no evolution of growth rates after year 150 (FL-FIX). (e) Ten random replicates for scenario FL-EVO and (f) 10 random replicates for FL-FIX. Only environmental and demographic stochasticity are included in the first 150 years of the simulation (·····), then also flood events are included and populations suffer massive mortality events.

between scenarios either (Mann–Whitney *U*-test, W = 25931·5, *P* > 0·05), although a slightly faster rebound was found in scenario FL-EVO (mean ± s.d. $\bar{t}_{10} = 2 \cdot 42 \pm 0 \cdot 35$) than in scenario FL-FIX ($\bar{t}_{10} = 2 \cdot 47 \pm 0 \cdot 39$).

Simulations performed with moderately stronger environmental stochasticity yielded essentially the same results.

DISCUSSION

The current understanding of how the interplay between density-dependent processes and endogenous disturbances, in particular strong disturbances causing massive mortalities, influences population dynamics and evolutionary processes of small populations is still very limited. It is expected that individuals will be adapted to the range of climate variability that they have experienced in the past, but this is clearly dependent

FIG. 4. Proportion of age 1 year fish in the *Salmo marmoratus* population prop(age-1) through simulation time
for the same (a)−(d) populations as in Figs 3 and 5. Ten year moving averages are represented as ⸻. In
the scenario with evolution of growth rates (FL-EVO), after reaching a quasi-stable population size, age-
and size-distribution (⸏⸏⸏⸏) prop(age-1) tends to increase through time, while it tends to remain stable or
decrease in the scenario with no evolution of growth rates (FL-FIX).

on the selective intensity of climate variability, as well as by its spatial and tempo-
ral properties. In particular, the eco-evolutionary dynamics of fishes in general and
salmonids in particular associated with an increase in the occurrence of massive mor-
talities induced by weather and climate extremes are largely unexplored.

The present work has shown how episodes of massive mortality affecting *S. mar-
moratus* populations have evolutionary consequences by selecting for faster-growing
fish, which in turn affects population dynamics and, when averaged over time,
population-level properties such as age and size distribution. While such demographi-
cally relevant changes might be expected to affect resilience as well, substantial effects
on the resilience of the simulated populations were not observed.

Historically, research on eco-evolutionary dynamics has focused on the eco-to-evo
pathways (*e.g.* density dependence), but the implications of the evolution of traits for
the dynamics of the population have been much less investigated (Carlson *et al.*, 2011).
This work offers some novel insights into the operation of the evo-to-eco pathway in
populations affected by catastrophic disturbances.

In the scenario with evolution of growth rates, in the eco-to-evo pathway,
phenotypes of fish (*i.e.* growth and body size) are shaped by selection deriving
from density-dependent processes, in which faster-growing fish are favoured at low
densities, as after severe flood events, while at higher densities a continuum of
slow-to-fast growing fish may coexist in the population (Mangel & Stamps, 2001).
Those selected phenotypes at low densities can then modify population dynamics (*i.e.*
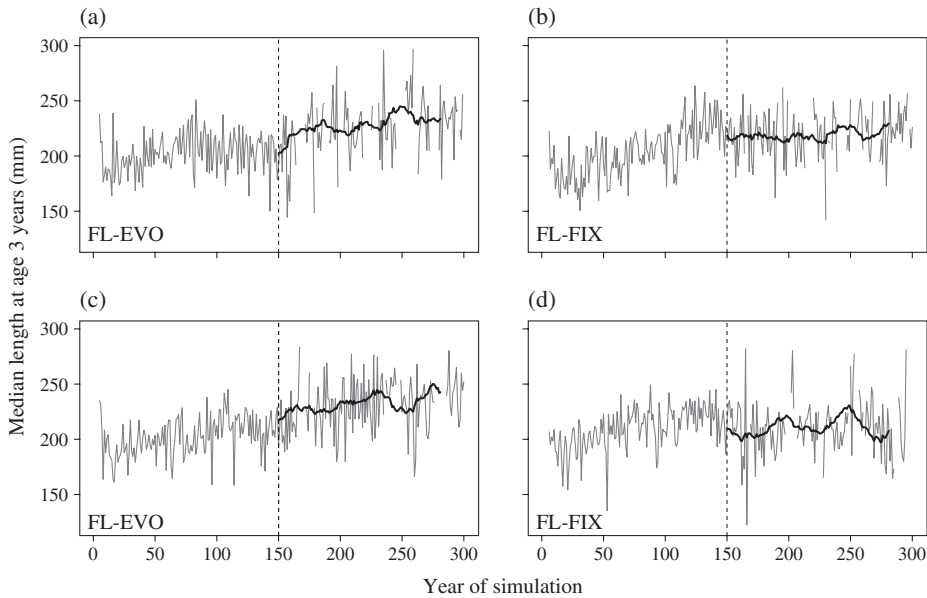evo-to-eco pathway). As a trade-off between growth and mortality was assumed, fish

FIG. 5. Median length at age 3 years ($\widetilde{L}_3$) through simulation time for the same *Salmo marmoratus* populations (a)–(d) as in Figs 3 and 4. ——, 10 year moving averages, while gaps in time series are due to absence in that year of age 3 year fish. In scenario with evolving growth rates (FL-EVO), after reaching a quasi-stable distribution in population size, age and size distribution at year 150 (- - - -), $\widetilde{L}_3$ tends to increase through time in the FL-EVO scenario, while it tends to remain stable or decrease in the scenario with no evolution of growth rates after year 150 (FL-FIX).

growing faster (larger ϕ) are more likely to die younger than fish growing slower, and this shifts the age-structure of the population towards younger fish as well as decreasing population size. The greatest increase in median length at age 3 years was observed in the first 50 years after the introduction of floods and then tended to level off as the population approached a new quasi-stable equilibrium in terms of age and size structure and population size.

The selection for faster life histories (*i.e.* earlier reproduction, faster growth and higher mortality risk due to a growth-mortality trade-off) did not increase the resilience of populations (*i.e.* time to recover from a critical population size to a safe population size) with respect to populations that did not evolve faster life histories, and in both cases (*i.e.* with or without evolution of growth rates), the number of extinctions was very low (Fig. 9). As previously shown (Vincenzi *et al.*, 2008a, 2010), this is likely to be ascribed to the relaxation of density-dependent limitations on early mortality and growth at low population densities. Although this result may seem counterintuitive, the lack of greater resilience to flood-induced massive mortalities of populations evolving faster life histories may be explained by (1) moderate heritability of growth rates, (2) the speed of recovery to a safe population size with respect to the evolution of faster life histories and (3) the contrasting demographic effects of massive mortality-induced evolution towards faster growth rates, but fewer old (and therefore potentially larger) spawners.
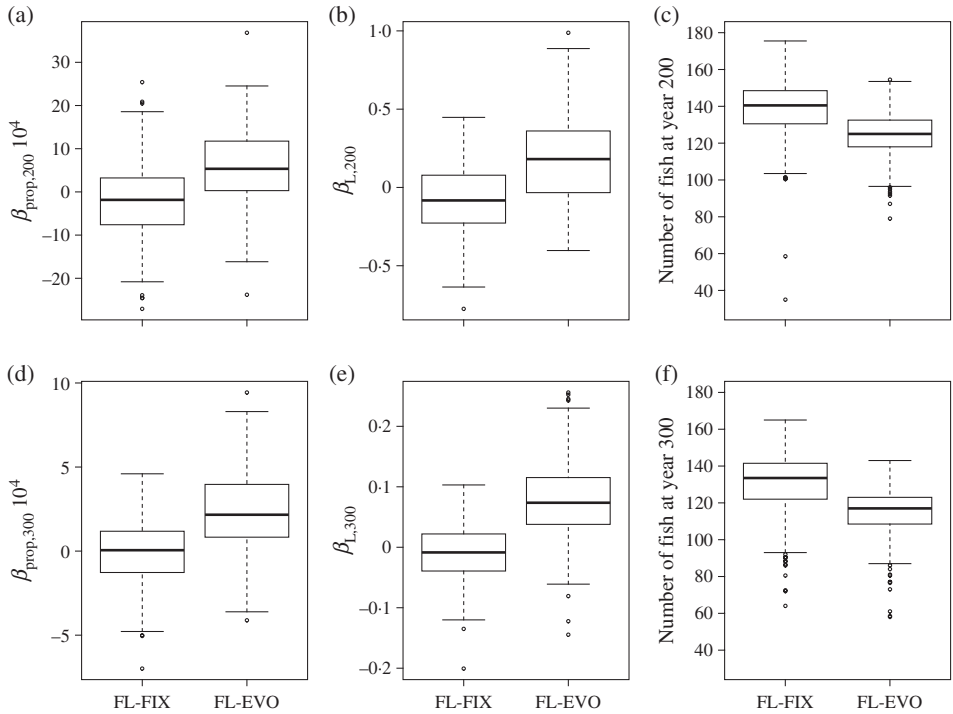
FIG. 6. Boxplots for (a) slope $\beta_{prop,200}$ of the regression of proportion of age-1 *Salmo marmoratus* prop(age-1) on simulation time from year 150 to 200 for the scenario with no evolution of growth rates (FL-FIX) and with evolution of growth rates (FL-EVO), (b) slope $\beta_{L,200}$ of the regression of median length at age 3 year $\widetilde{L}_3$ on simulation time from year 150 to 200, and (c) median population size from year 175 to year 200 years of simulation time, (d) slope $\beta_{prop,300}$ of the regression of prop(age-1) on simulation time from year 150 to 300, (e) slope $\beta_{L,300}$ of the regression of $\widetilde{L}_3$ on simulation time from year 150 to 300 and (f) median population size from year 275 to year 300 of simulation time. For all boxplots, median = ——, 25th to 75th quantile = □, 2·5–97·5% quantile = ⊢----⊣, outliers = ○.

When > 10–20 years elapse between floods, slower growing fish are progressively introduced back in the population since heritability of body size at age is within 0·2–0·4 and the fitness landscape changes with population density, favouring slower-growing longer-living fish at high population densities (Vincenzi *et al.*, 2012*a*). This limits the potentially faster rebound to pre-event population size level with respect to the scenario without evolution of growth rates. In other words, the differences between the two scenarios in terms of age-structure and growth potential, albeit maintained over time as shown by the positive slopes of the linear models for proportion of young fish and median length at age 3 years, are mostly in the few years following the flood. Moreover, recovery to a safe population size of 50 females happens in 2–3 years depending on the severity of collapse and therefore recovery is usually faster than the selection for faster life histories.

In addition, while median length of age 3 year fish is greater for evolving populations, but only slightly, on the order of 2–5% greater median length than in non-evolving populations [Fig. 7(a)], non-evolving populations tend to include a greater proportion of older females given the presence of a growth-mortality trade-off. Thus, as in the
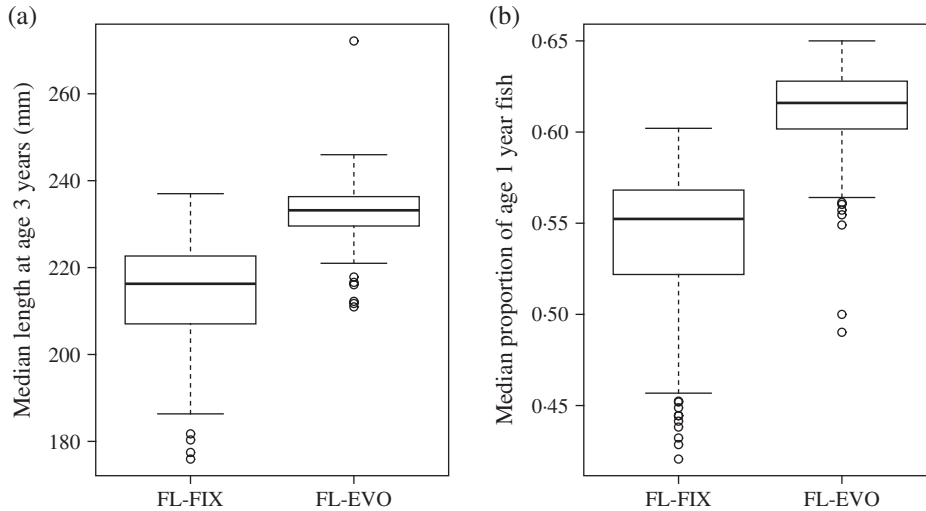
FIG. 7. Boxplot of (a) median length at age 3 years $\widetilde{L}_3$ and (b) proportion of age 1 year female *Salmo marmoratus* prop(age-1) in the last 50 years of simulation time for scenario with evolution (FL-EVO) or no evolution (FL-FIX) of growth rates. Median = ⎯⎯, 25–75th quantile = □, 2·5–97·5% quantile = ⊢⎯⎯⊣, outliers = o.

simulation flood events did not directly (*i.e.* in terms of different survival probabilities for individuals with different phenotypes) select for body size and growth rates, non-evolving populations are more likely to include older and larger females among the ones surviving the flood than evolving populations, with potentially higher egg production immediately after the catastrophic event for the non-evolving populations.

In both scenarios, the relaxation of density dependence increases growth and decreases early mortality and possibly age at sexual maturity (Vincenzi *et al.*, 2008*a*, 2012*a*), and given the relatively high egg production of *S. marmoratus* at low densities with respect to the number of fish needed to reach a safe population size, a few females may be sufficient in either scenario for a fast recovery to a safe population size in a few years (Vincenzi *et al.*, 2008*a*). Thus, there may be limited potential to evolve further resilience, in particular given the functional form of the growth-mortality trade-off that was used in the model.

Although the evolutionary response to floods led to slightly smaller population sizes over simulation time for evolving populations, this did not affect the realized extinction risk. This seems to reflect population sizes in the absence of floods generally large enough to be safe from the effects stochastic fluctuations, combined with the rapid recovery from floods made possible by the relaxation of density dependence at very low densities. With mass mortality events, population size after a flood was only loosely correlated with population size before the flood.

Studies have investigated traits conferring greater resilience to exploited marine and anadromous fish populations. Hutchings & Reynolds (2004) found for fishes that the ability to buffer the effects of external forces is largely due to the population's age-structure and the species' life-history traits. For example, populations with multiple age-classes spawning are more likely to resist, and recover from, prolonged periods of adverse conditions for reproduction than species with a limited window for reproduction [*e.g.* sardine *Sardina pilchardus* (Walbaum 1792)] (Hidalgo *et al.*,
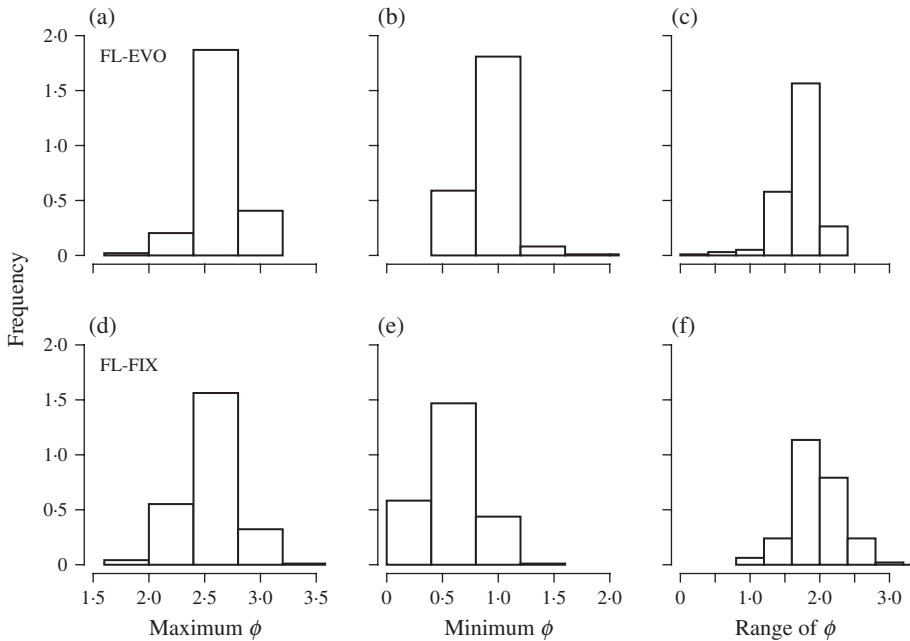
FIG. 8. Histograms representing the distribution across replicates of (a), (d) maximum, (b), (e) minimum and range (c), (f) of *Salmo marmoratus* growth potential ϕ in the scenario with (a), (b), (c) evolution (FL-EVO) or (d), (e), (f) no evolution (FL-FIX) of growth rates at the end of simulation time.

2011). In addition, Greene *et al.* (2010) found for nine Bristol Bay sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) populations that life-history diversity can both increase production and buffer population fluctuations. Great differences exist between exploited marine and anadromous populations and unexploited stream-dwelling populations in terms of population size, additive genetic variance (typically increasing with population size), spatial extension of habitat, movement and selective pressures (*e.g.* preferential human exploitation of fast-growing fishes in exploited marine populations). Thus, the role of evolutionary processes in the resilience of exploited marine and anadromous populations is difficult to compare with that of unexploited stream-dwelling populations.

Other studies are needed before ruling out the possibility that evolution of life histories may increase population resilience to catastrophic and unselective disturbances. In the present work, for simplicity, only floods occurring before spawning were considered. This prevents any flood-induced loss of eggs. While floods have historically occurred in the region where *S. marmoratus* live in October to early November, thus before spawning, in the last decade spring floods began to occur. Field observations for *S. marmoratus* (Pujolar *et al.*, 2011) and a wealth of studies for other salmonid species (Hanson & Waters, 1974; Hoopes, 1975; Pearsons *et al.*, 1992; Pert & Erman, 1994) suggest that both eggs and young fish are more vulnerable to floods than adults and that there might be zero recruitment when floods occur after spawning. In addition, consecutive floods have recently occurred in a very short period of time in the Slovenian streams where *S. marmoratus* live (Pujolar *et al.*, 2011; Vincenzi *et al.*, 2012*c*). For example, *S. marmoratus* living in the Lipovscek Stream successfully
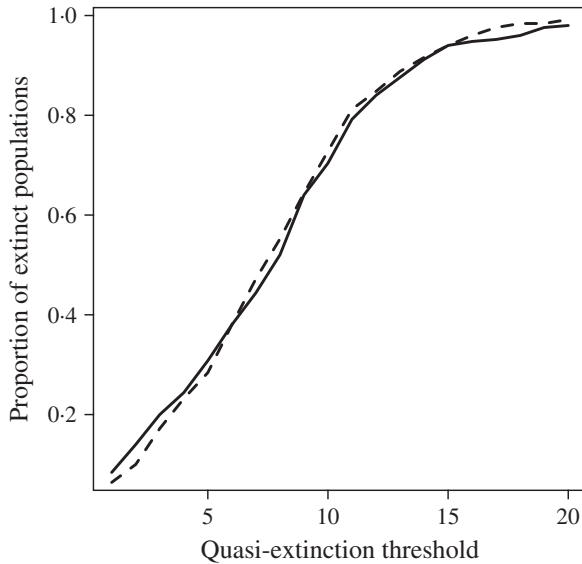
FIG. 9. Proportion of *Salmo marmoratus* populations going quasi-extinct for quasi-extinction thresholds ranging from one to 20 females in the population. Only four and nine replicates went extinct (number of adults = 0) in scenario with evolution (FL-EVO; _ _ _) and no evolution (FL-FIX; ——) of growth rates.

recovered after a flood in 2004, but in September 2007, a new severe flood caused a 90% reduction in population size. After a new flash flood in 2009 and a moderate flood in 2010, the population has been reduced to <10 individuals. Thus, interesting questions are whether the evolution towards faster life histories may increase resilience when floods occur with increased frequency, as expected with climate change (IPCC, 2007), and with reduction or complete loss of eggs due to their occurrence in spring.

In the model presented in this work, *S. marmoratus* growth depended on individual growth potential and population density during the first year of life, but additional processes are likely to contribute to growth dynamics, and they might be relevant for population resilience to catastrophic floods. The importance of early growth for lifetime growth and size at age has also been recently shown for *S. fontinalis* living in West Brook (MA, U.S.A.) (Letcher *et al.*, 2011), but compensatory growth, although not observed so far in *S. marmoratus* population, may also evolve (Mangel & Munch, 2005). In addition, although salmonid growth and life histories have been studied in a variety of species, most of the studies have focused on single factors affecting growth, like temperature, flow or density, and only a few studies have investigated the effects on growth of the interaction between them (Cunjak *et al.*, 1998; Rand *et al.*, 2006; Stradmeyer *et al.*, 2008). Recently, it has been found in juvenile Atlantic salmon *Salmo salar* L. 1758 that effects of population density are substantially weaker than effects of discharge and temperature across all seasons (Davidson *et al.*, 2010). This is particularly important, because climate change-induced increased frequency, intensity and altered timing of floods event are likely to be accompanied by an increase in water temperature and a modification of the prey base. Thus, further investigations are needed to understand the interplay between plastic growth responses and selective processes in a changing climate.

DATA

Data and code to reproduce the analyses presented in this work can be downloaded at: http://figshare.com/articles/Data_for_the_ms_Evolution_of_growth_rates_and_resilience_to_massive_mortality_events_/747616

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