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POPULATION ECOLOGY - ORIGINAL PAPER

Selective consequences of catastrophes for growth rates in a stream-dwelling salmonid

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Abstract Optimal life histories in a fluctuating environment are likely to differ from those that are optimal in a constant environment, but we have little understanding of the consequences of bounded fluctuations versus episodic massive mortality events. Catastrophic disturbances, such as floods, droughts, landslides and fires, substantially alter the population dynamics of affected populations, but little has been done to investigate how catastrophes may act as a selective agent for life-history traits. We use an individual-based model of population dynamics of the stream-dwelling salmonid marble trout (*Salmo marmoratus*) to investigate how trade-offs between the growth and mortality of individuals and density-dependent body growth can lead to the maintenance of a wide or narrow range of individual variation in body growth rates in environments that are constant (i.e., only demographic stochasticity), variable (i.e., environmental stochasticity), or variable with catastrophic events that cause massive mortalities (e.g., flash floods). We find that occasional episodes of massive mortality can substantially reduce persistent variability in individual growth rates. Lowering the population density reduces density dependence and allows for higher fitness of more opportunistic strategies (rapid growth and early maturation) during the recovery period.

Keywords Catastrophes · Selection · Growth rates · Marble trout · Variable environment

Introduction

Disturbances have ecological consequences, as they alter populations, communities and trophic structure (Collins et al. 1981; Sousa 1984; Wootton 1998a, b). In addition, disturbances may have evolutionary consequences, as they change population gene frequencies (Vrijenhoek et al. 1985) by shaping and constraining life-history strategies (Levins 1968; Schaffer 1974; Lytle 2001) both in the short run (Boyce et al. 2006) and over longer time scales (Ruzzante et al. 2008), and by selecting for particular morphologies and behaviors (Meffe 1984; Gelwick 1990; Lytle 1999). A number of studies have investigated the consequences of episodes of massive mortality (catastrophes) on population dynamics and persistence across several taxa (e.g., Mangel and Tier 1994), but most investigations to date have not considered how catastrophes shape life histories. We interpret "catastrophes" as including physical

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factors such as storms, flood and droughts, biological factors such as diseases or invasions by a new competitor or predator, or anthropogenic perturbations of the environment.

In streams, fluctuations in flow and extreme flows are primary sources of environmental variability and disturbance, respectively (Poff and Ward 1989). Extreme flows span a broad frequency, severity, timing and predictability ranges. To mitigate their ecological impact, species may exhibit various adaptations that result from trade-offs among growth, reproduction, and survival (Arendt 1997). According to life-history theory, large and predictable variations in the flow regimes of streams can have important evolutionary consequences by selecting for life histories that are synchronized to either avoid or exploit the direct and indirect effects of extreme flows (Lytle and Poffs 2004). In addition, Meffe (1984) found that behavioral differences between native and nonnative species represent the mechanism that is primarily responsible for the observed patterns of differential removal of native and nonnative fishes during floods.

On the contrary, large but unpredictable flow events have low selective consequences for the affected populations, even though they may induce massive mortalities (Lytle 2000). Although no optimal strategy for life-history timing can evolve to avoid the unpredictable floods or droughts, theory suggests that bet-hedging strategies might evolve for organisms that produce eggs (Lytle and Poffs 2004), since spreading the reproductive output over an extended period increases the chances that a portion of the reproductive output will result in the successful production of offspring (Spranza et al. 2000; Durham and Wilde 2005). The lifespan of an organism is likely to affect the strength of selection, since the number of disturbances encountered by an organism is related to its lifespan (Lacey et al. 1983; Venable and Brown 1988; Turner et al. 1998). However, even in the presence of adaptations that mitigate the ecological effects of disturbances, flash floods and debris flows associated with short, very high-intensity rainfalls (Marchi et al. 2010) will cause fish populations to experience massive density-independent mortality, followed by an increase in per capita resources and a high population growth rate as they recover from the collapse. After the occurrence of a catastrophic event, selection is thus predicted to favor individuals with a high capacity to increase in population size (*r* selection, MacArthur and Wilson 1967).

In freshwater fishes, floods and droughts play an important role in the regulation of population dynamics (e.g., Elliott et al. 1997; Jensen and Johnsen 1999), to the extent that in high-gradient streams, fish life histories can be largely shaped by extreme flow events (Meffe 1984; Lytle 2000; Lytle and Poffs 2004). The direct and short-term effects of floods are largely a result of high-water velocities and sediment movement, which cause fish displacement and death, and a therefore a collapse in population size (e.g., Collins et al. 1981). Variation in body size may have important implications for the population structures and dynamics of fishes, since body size is related to a variety of ecologically important characteristics such as survival and fecundity rates, competitive and predatory ability, foraging behavior and body growth rates (Wootton 1998a, b). Theoretical understanding of the relationship between size-dependent ecological performance and population dynamics is still rather limited (De Roos et al. 2003). The density dependence of body growth and the large variations in population density—even in the absence of catastrophic events—that are often observed in streams make observing and disentangling the relative contributions of density and individual growth rates to the realized growth of individuals particularly challenging. Moreover, density-dependent processes are also likely to shape life histories (Engen et al. 2005; Bonenfant et al. 2009). Recently, Lande et al. (2009) showed that the magnitude of environmental stochasticity and the form of the density dependence govern the trade-off between *r* and *K* selection.

Vincenzi et al. (2008a) used a simulation analysis to conclude that density-dependent body growth in freshwater fish may increase the resilience of populations to catastrophes (i.e., flash floods and debris flows inducing massive mortalities). Since body size is a key determinant of age at maturity and egg production, the relaxation of density-dependent pressure after an episode of massive mortality can increase body growth rates and consequently the reproductive output during the years immediately following the catastrophe. Large variations in population densities may affect individual growth, age at maturity, and longevity, so that episodes of massive mortality may lead to compensatory changes in life histories through phenotypic plasticity or evolutionary adaptations, with obvious repercussions for both ecological theory and fisheries management.

In this work, we use an individual-based model to explore how density-dependent processes (survival and growth) and different environmental conditions can create different selective environments for individual growth rates. We investigate environments that are constant (i.e., only demographic stochasticity), variable (i.e., including environmental stochasticity) and variable with the occurrence of unpredictable catastrophes (i.e., flash-flood events). We tuned model parameters based on data from populations of marble trout (*Salmo marmoratus*), an endangered stream-dwelling salmonid for which autumnal flash floods and debris flows are a major threat to its viability (Vincenzi et al. 2008a, b, 2010).

Materials and methods

Model of population dynamics

The individual-based model we use here is an extension of the model of population dynamics of marble trout by Vincenzi et al. (2008a), accounting for variability in individual growth rates among individuals living in the same population. In Electronic supplementary material 1, we provide a description of the model according to the ODD (overview, design concepts, details) protocol for describing individual-based and agent-based models (Grimm et al. 2006, 2010).

We use the model to explore the distribution of individual growth rates in a population of marble trout, a freshwater salmonid. Populations of this species can evolve in three different environments: constant with stochastic birth and death processes (CON); variable (i.e., with environmental stochasticity, VAR); or with the occurrence of catastrophic events (i.e., flash floods and debris flows) causing sudden and massive mortality (CAT). We model only females. Each fish is characterized by the individual (somatic) growth parameter ϕ, which affects both its survival and growth. We refer to individuals in their first year of life (from age zero to their first winter) as juveniles, fish that are at least one year old but are not reproductively active as immature, and adults are fish that have reached sexual maturity (Fig. 1). We parameterized the model with reference to the marble trout population of Zakojska (Slovenia, Vincenzi et al. 2008a).

Body growth

In marble trout, the density conditions experienced during the first year of life have a long-lasting influence on the body growth of fish (Vincenzi et al. 2008c; see Harrison et al. 2011 for a review of carry-over effects and their effects on individual fitness). We model length-at-age as von Bertalanffy growth, with the asymptotic size set by the density experienced in the first year of life. Thus, for an individual of age a, length growth rate ϕ, density of marble trout $\geq$ age 1 during its first year of life (density as an underyearling) D_U (ind. m^{-2}), and strength of density dependence γ, the length-at-age is

$$L(a|D_U,\gamma,\phi) = \frac{L_\infty}{1+\gamma D_U}\left(1-e^{-k\phi(a-a_o)}\right). \qquad (1)$$

We estimated model parameters by nonlinear regression using data in Vincenzi et al. (2008c). The density during later years and at maturation seem to play only a minor role in determining growth trajectories (Vincenzi et al. 2008c), and thus for simplicity they were not considered in this model of body growth. The growth parameter ϕ is a multiplier of the growth rate k and is equal to 1 for the population of marble trout ("base case") used to tune the model parameters (Fig. 2). We assume that individuals living sympatrically may have different individual growth rates ranging from 0 to 2.

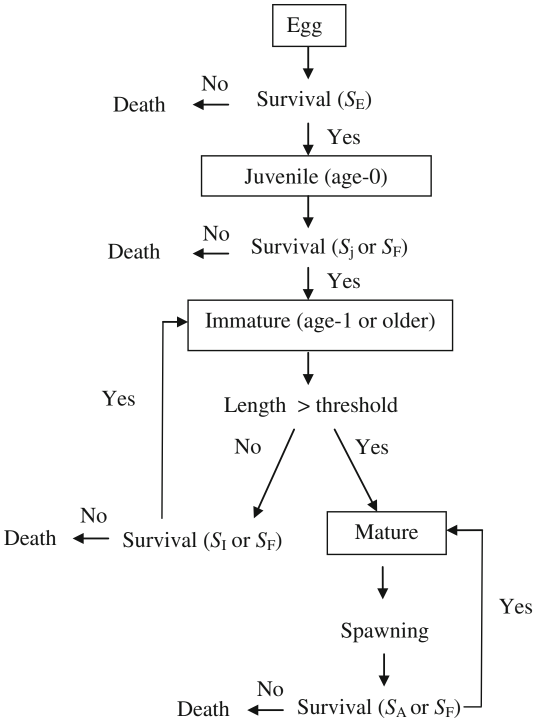

Fig. 1 Schematic representation of the model of the population dynamics for marble trout *Salmo marmoratus* living in Slovenian streams. In the case of flood events, the juvenile survival S_j, the immature survival S_I, and the adult survival S_A are replaced with the survival S_F

Reproduction

A tight relationship linking female length to sexual maturity and egg production is commonly observed in salmonids (e.g., Hendry and Stearns 2003). Vincenzi et al. (2008b) found in farm experiments that the number of eggs produced by marble trout E was related to the body length L of the female by the linear relationship

$$E = \alpha_E + \beta_E L, \qquad (2)$$

where $\alpha_E < 0$, $\beta_E > 0$, and $\frac{|\alpha_E|}{\beta_E}$ is the length at sexual maturation. The form and parameters of Eq. 2 were estimated based on data from experiments in a fish farm (Vincenzi et al. 2007a). Based on Eq. 2, the length at maturity is invariant to differences in growth rates, and thus the age at maturity is both ϕ and density dependent (Fig. 2). Length at maturity is insensitive to variation in density in many fish populations, although the corresponding age at maturity can change substantially as a

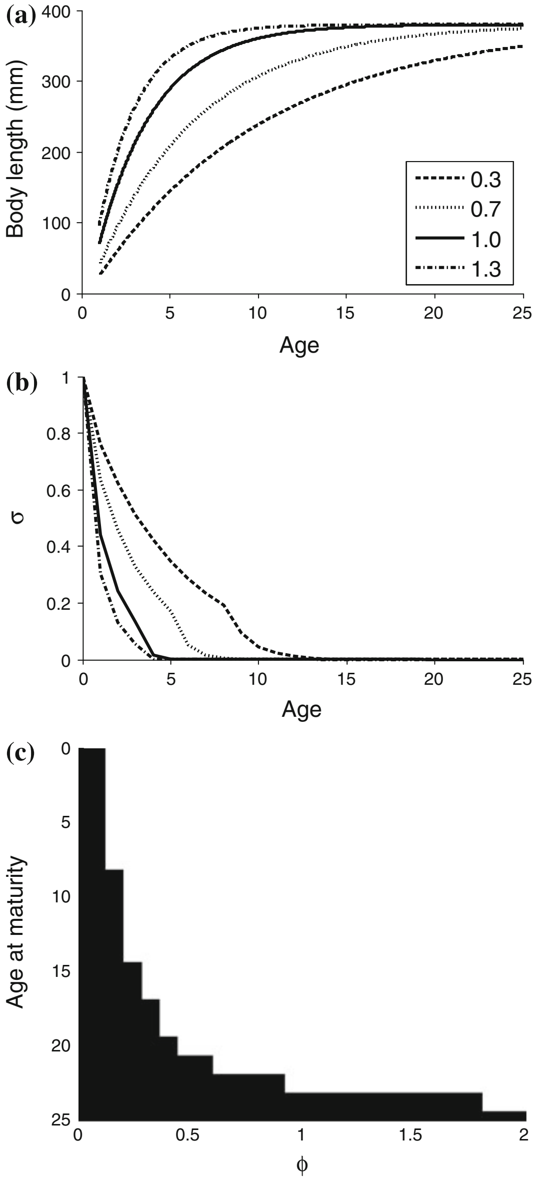

Fig. 2 **a** Growth trajectories, **b** survival curves, and **c** age at maturity for fish with different individual growth rates as described by the growth parameter ϕ, namely 0.3, 0.7, 1 ("base case"), and 1.3. The density of fish $\geq$ age 1 in the first growth period D_u, the density of juveniles D_j, and the density of fish $\geq$ age 1 D_A were all set to 0.5. Survival to age zero was normalized to 1. Survival curves show a distinct drop when the fish reach sexual maturation. In **c**, the *white region* identifies sexual maturity

result of density dependence in growth (Mangel and Abrahams 2001; Lorenzen 2005). A number of studies on salmonid species have reported a general correlation between rapid growth and early sexual maturation (e.g., Hutchings and Jones 1998; Utrilla and Lobon-Cervia 1999), with slow-growing fish delaying sexual maturation in order to reach the minimum size required for gonad development.

We assume that fish spawn annually from maturity until death. In the wild, approximately half of mature females reproduce successfully each year (Meldgaard et al. 2007; A. J. Crivelli, unpublished data), and we use Bernoulli trials ($p = 0.5$) to determine if eggs produced by the individual female are viable and thus included in the egg pool. Variation in growth patterns from differences in either individual growth rate or population density affect the reproductive value of individuals.

Transmission of the growth parameter ϕ

In order to facilitate the interpretation of results, we assume that the newborn perfectly inherits the growth parameter ϕ from the parent, but we introduce "mutation" rates to allow for small variations in ϕ over the simulation time; thus

$$\phi_O = \begin{cases} \phi_p & \text{with } p = 0.98 \\ \min[|\phi_p + u|, 2] & \text{with } p = 0.02, \end{cases} \qquad (3)$$

where u is randomly drawn from the uniform distribution over the interval [−0.2, 0.2] and ϕ_p and ϕ_o are the growth parameters of the parent and offspring, respectively. We performed simulations with reduced heritability of ϕ to assess the robustness of the results (see "Sensitivity analysis").

Survival

We assume that egg to age-zero survival S_E is independent of density (J-F. Rubin et al., unpublished manuscript) and constant across ϕ, while juvenile (from age-zero to the first winter) survival S_j is density dependent:

$$S_\mathrm{j}(M, w_\mathrm{j}, D_\mathrm{j}, \phi) = \mathrm{e}^{-M(1+\omega_j D_\mathrm{j})\phi}, \qquad (4)$$

where M is the annual mortality when densities approach zero, D_j is the density of juveniles (ind. m^{-2}), and ω_j describes the strength of the density dependence for juvenile survival. We estimated the parameters of the model for first-year survival from the results of Vincenzi et al. (2007a).

The growth parameter ϕ determines the growth–mortality trade-off for the individual. The classic trade-off between growth and mortality arises in the case of foraging under the risk of predation, in which animals may grow at optimal—rather than maximal—growth rates due to predation risk (e.g., Arendt 1997). However, several recent studies have indicated that various trade-offs may limit the benefit of rapid growth (Arendt 1997; Mangel and Stamps 2001; Post and Parkinson 2001; Munch and Conover 2003; Biro et al. 2005; Stoks et al. 2005), and many functions or traits may be reduced or compromised or when individual growth rates are maximized (Roff 2002). For simplicity, and in the absence of empirically validated models for marble trout, we assume a linear effect of ϕ on instantaneous mortality rate.

Vincenzi et al. (2008a) did not find any evidence for size-selective mortality, so S_{j} is independent of size. The annual survival S_{I} for sexually immature trout is therefore

$$S_{\mathrm{I}}(M, \omega_{\mathrm{A}}, D_{\mathrm{A}}, \phi) = \mathrm{e}^{-M(1+\omega_{\mathrm{A}} D_{\mathrm{A}})\phi}, \tag{5}$$

where D_{A} is the density of fish $\geq$ age 1 (ind. m^{-2}), and ω_{A} characterizes the strength of the density dependence for survival. We estimated the parameters of Eq. 5 from mark–recapture data (Vincenzi et al. 2008a; S. Vincenzi, unpublished manuscript). As is commonly observed in stream-dwelling salmonids, the strength of density-dependent survival is greater for juveniles than for adults ($\omega_{\mathrm{j}} > \omega_{\mathrm{A}}$).

For sexually mature trout, we modify Eq. 5 to account for spawning mortality:

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

where v characterizes the cost of reproduction. We obtained the value of v from experiments performed in the fish farm (S. Vincenzi and A. J. Crivelli, unpublished data).

If α is the age of sexual maturity, survival from egg to age a in a constant environment is then

$$\begin{cases} \sigma_a = S_E S_j \prod^{a-1} S_I & \text{if a } < \alpha \\ \sigma_a = S_E S_j \prod^{m-1} S_I \prod^{a-m} S_A & \text{if a } > \alpha, \end{cases} . \tag{7}$$

We model the survival probability S_{F} in case of a flood event (for juveniles, immature and adult fish alike) as follows:

$$S_{\mathrm{F}} = \mathrm{e}^{-M_{\mathrm{F}}(R)}, \tag{8}$$

where $M_{\mathrm{F}}(R)$ is the mortality induced by the flood event, which depends on the rainfall R. In the case of $R > 400$ mm, we assume that mortality is independent of the growth parameter ϕ, density and age. We developed the relationship between the intensity of a flood event and the mortality M_{F} using empirical data and expert knowledge, with the October rainfall recorded in the study area used as a proxy for a flood event. For $R > 400$ mm,

$$M_{\mathrm{F}}(R) = \min[\alpha_F + \beta_F R, M_{\max}], \tag{9}$$

were R is the October rainfall (mm). Rainfall greater than 1,000 mm (for which $M_{\mathrm{F}}(R) = M_{\max}$) has a recurrence time of approximately 20 years.

Simulation scenarios

We ran the model for 500 replicates for each of the three scenarios CON, VAR and CAT.

We started each simulation with 350 individuals randomly aged between 0 and 6, where each individual had a randomly assigned growth parameter ϕ from a uniform distribution bounded between 0 and 2. In CON, we only included demographic stochasticity. In VAR, we modeled environmental stochasticity by randomly drawing values of model parameters at each time step of the simulation from the uniform distribution [0.95 P, 1.05 P], where P is the parameter value. We chose the uniform distribution for simplicity and the interval [0.95 P, 1.05 P] to clearly separate the effect of environmental variability from the effect of catastrophic events (but see "Sensitivity analysis"). In CAT, we modeled catastrophes (i.e., flash floods and debris flows) by randomly drawing at each time step a rainfall value for October R (in mm) from the empirical lognormal distribution fitted to rainfall data recorded in the study area from 1961 to 2007 ($\mu = 300$ mm, SD = 328; both parameters were on the arithmetic scale) (Vincenzi et al. 2008a). If the rainfall was greater than 400 mm, a catastrophic event occurred and the survival of the fish was modified as described above. We provide values of the model parameters in Table 1. We computed densities at each time step by dividing twice the number of individuals (for a 1:1 sex ratio, since we modeled only females) by the surface area of the stream. Although flash floods and debris flows can substantially modify the habitat (by altering biotic communities and the physical structures of streams, and by creating or destroying habitat), their consequences are largely unpredictable. Accordingly, we assumed the surface area of the stream to be constant over time and equal to 900 m^2, and we allowed the random variation in vital rates to incorporate the effects of floods on the habitat. We computed the population size and distribution of individual growth rates in the fall, before spawning. We considered populations with fewer than 5 females > age zero to be extinct, and excluded such replicates from the analysis of the results. At each time step, Bernoulli trials defined if an individual survived or died. Eggs were spawned in the fall, and age-zero individuals emerged during the following year in late spring-early summer. We assumed that flood events would impact the population after the spawning period.

We ended the simulation when the distribution of growth parameters ϕ was quasi-stable (ϕ_{qs}), as characterized by the following conditions. For two time steps 25 years apart (ϕ_{t}, $\phi_{\mathrm{t+25}}$), both the minimum and the maximum values of (ϕ_{t}, $\phi_{\mathrm{t+25}}$) coincided, and the P value of the Kolmogorov–Smirnov (KS) test for differences between ϕ_{t} and $\phi_{\mathrm{t+25}}$ was $\geq$0.7. We arbitrarily chose this

Table 1 Parameter values for the model of population dynamics

Model	Parameter	Estimates	Range for sensitivity analysis	Source
Density-dependent body growth	γ	0.1	0–0.2	Data from Vincenzi et al. (2008c)
	L_∞	380		
	K	0.34		
	a_0	0.34		
Reproduction	α_E	−750		Vincenzi et al. (2008b)
	β_E	3.8		
Mortality	σ_E	0.035		Data from Vincenzi et al. (2008a, b) and S. Vincenzi and A. J. Crivelli, unpublished data
	M	0.48		
	ω_j	3		
	ω_A	1.2		
	v	2		
Floods	μ	298	200–300	Data from Vincenzi et al. (2008a)
	SD	327		
	α_F	1.7		
	β_F	0.0018		
	M_{max}	2.8		

In scenarios with a variable environment (VAR) and a variable environment with the occurrence of floods (CAT), we drew values randomly from a uniform distribution over [0.95P, 1.05P], where P is the parameter estimate. Values of μ that were greater than 300 mm were not used in the sensitivity analysis due to the high number of extinctions caused by the simulated flood events

P value after a preliminary exploration of model simulations (see "Sensitivity analysis").

Preliminary explorations of replicates guided the choice of appropriate and informative metrics to assess the population-level response in the growth parameter ϕ (Fig. 3). We fitted both a bimodal and unimodal Gaussian mixture model to ϕ_{qs} and used the AIC to assess which of the two models better explained the data. A unimodal distribution of ϕ_{qs} might be seen as directional or stabilizing selection, while the bimodal distribution of ϕ_{qs} might be seen as disruptive selection. We estimated the location of the peak (or peaks, depending on the selection of uni- or bimodality) in ϕ_{qs} through a Gaussian mixture model, recorded max(ϕ_{qs}) and min(ϕ_{qs}), and computed the range of growth parameters in the population at t_{qs} as max(ϕ_{qs}) – min(ϕ_{qs}). Finally, we recorded the time taken to reach a quasi-stable distribution t_{qs}.

Sensitivity analysis

We assessed the robustness of the results to alternative assumptions regarding the shape of the initial distribution of ϕ (uniform, beta, and lognormal) and the number of individuals (ranging from 300 to 500) in the first year of the simulation. We performed simulations with different P values of the KS test ranging from 0.5 to 0.8 to test if alternative P values substantially altered the time t_{qs} needed to reach a quasi-stable distribution. We widened the interval of uniform distribution to [0.9P, 1.1P] for estimates of model parameters (Table 1) and tested whether it influenced the simulation results of the scenario VAR. Then, we tested the sensitivity of the model's results to variations in the strengths of density-dependent body growth (γ) and flood events (μ) (Table 1) using logistic and ordinary least-squares regressions. We used logistic regression with a logit link function when the categorical variable ϕ_{qs} (bimodal = 1 and unimodal = 0, see Fig. 3) was the response variable. We used ordinary least-squares regression when the response variables were (a) the range of growth rates at t_{qs} (b) max(ϕ_{qs}), and (c) min(ϕ_{qs}). For all regressions, the strength of the density-dependent body growth (γ) and flood events (μ) were the independent variables. We started with values of γ and μ and their interaction predictors and then proceeded with stepwise selection. Finally, we carried out simulations with reduced heritability of ϕ (see Electronic supplementary material 2).

Results

When flood events were explicitly included in the simulations, the population suffered episodes of massive mortality that caused the population size to collapse (CAT, Fig. 4). On the contrary, when flood events were not included (CON and VAR environments), the simulated populations did not show dramatic year-to-year fluctuations in size. In the example provided for CON and VAR, the selection of growth parameters alters the population size and population dynamics over the simulation time (see Electronic supplementary material 3). Since no ceiling is

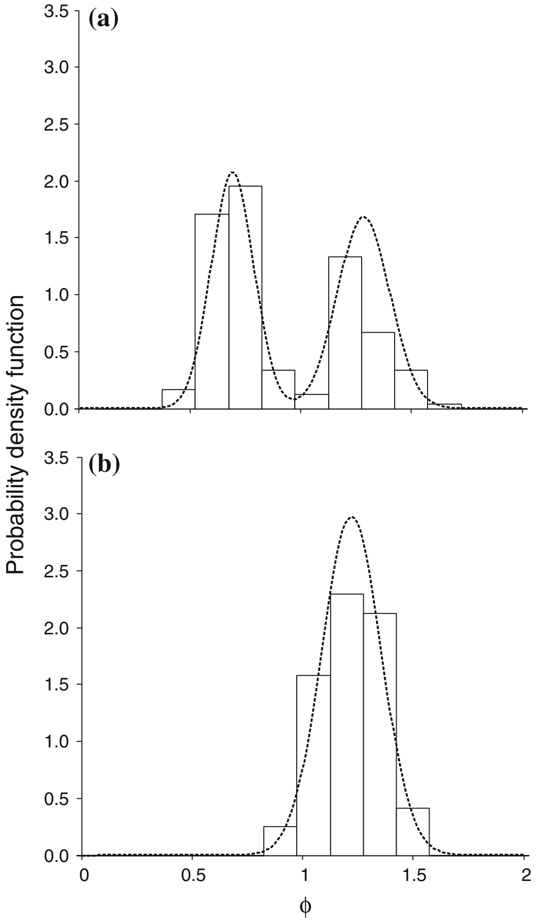

Fig. 3 Examples of two quasi-stable distributions of the growth parameter ϕ_{qs} ($n = 160$), along with the probability density function of the bi- or unimodal distribution that was the best fit to ϕ_{qs} according to the AIC. **a** ϕ_{qs} is described by a bimodal Gaussian mixture model (lower peak of $\phi_{qs} = 0.7$, higher peak $= 1.3$, $\min(\phi_{qs}) = 0.35$, $\max(\phi_{qs}) = 1.7$, range of $\phi_{qs} = 1.35$). **b** ϕ_{qs} is described by a unimodal Gaussian mixture model (peak of $\phi_{qs} = 1.3$, $\min(\phi_{qs}) = 0.85$, $\max(\phi_{qs}) = 1.6$, range of $\phi_{qs} = 0.75$). In the sensitivity analyses, ϕ_{qs} would be recorded as 1 in **a** and as 0 in **b**

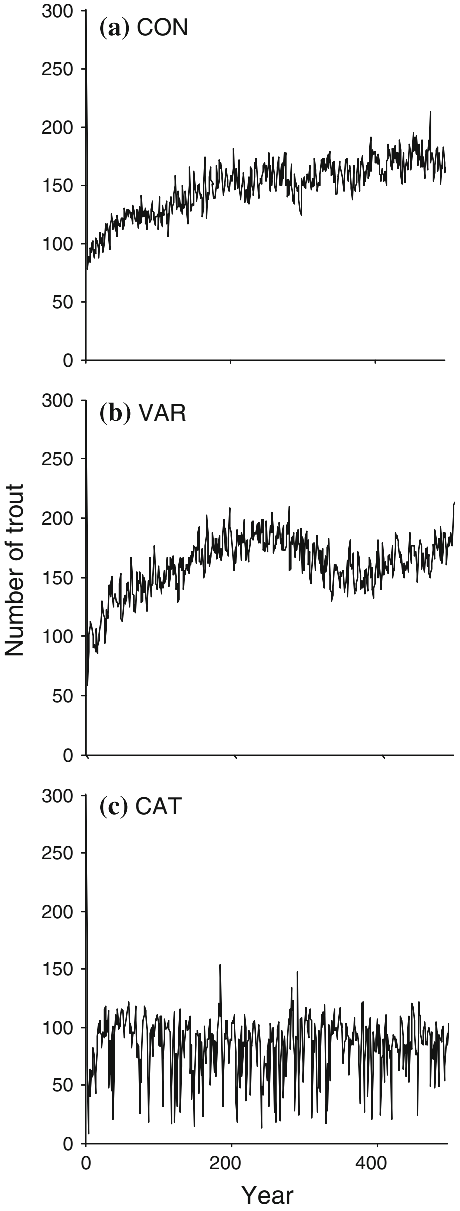

Fig. 4 Population sizes of marble trout over 500 years in random replicates for **a** a constant environment (CON), **b** a variable environment (VAR), and **c** a variable environment with the occurrence of flood events (CAT)

imposed on the population size, the distribution of ϕ in the population influences the number of eggs produced, the survival of the fish, and ultimately the population size. In CON and VAR environments, the population never went extinct, while around 10% of the CAT simulation replicates went extinct as a result of a flood event causing massive mortality.

In CON and VAR environments, the distribution of growth parameters at the end of the simulation time ϕ_{qs} was better explained by a bimodal distribution in about 90 and 80% of cases, respectively (Fig. 5), while unimodality ϕ_{qs} was observed in about 80% of the cases in CAT. The distribution of the range of ϕ_{qs} showed that the co-existence of slower and faster growers was more likely in CON and VAR scenarios than in the CAT scenario. Very fast growers ($\phi \to 2$) were not able to persist in any of the three scenarios. The absence of episodes of massive mortality allowed the persistence of slow growers in some replicates, particularly CON and VAR. In all three environments, the peak of ϕ_{qs} in the unimodal cases was approximately 1. In the case of bimodality, a higher peak was located for all scenarios at approximately the same values of ϕ as in the unimodal cases. The lower peak in the bimodal cases was basically located in the same position in all three scenarios. The time t_{qs} needed to achieve a quasi-stable distribution of growth parameters was always less than 500 years, but

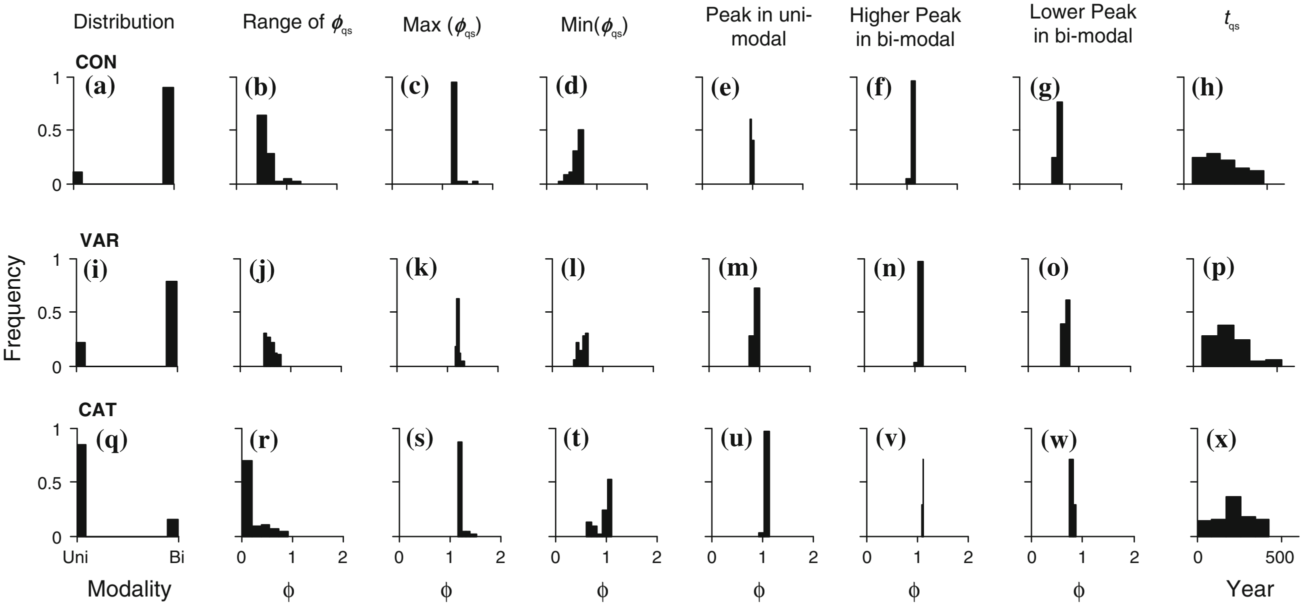

Fig. 5 The distributions of metrics computed on replicates ($n = 100$) in the three scenarios: **a**–**h** constant environment (CON); **i**–**p** variable environment (VAR); **q**–**x** variable environment with the occurrence of flood events (CAT)

no distinct pattern was observed among scenarios. In Fig. 6 we show typical selection dynamics observed in a simulation with environmental stochasticity and the occurrence of flood events (scenario CAT). Extremely fast ($\phi \to 2$) and slow growers ($\phi \to 0$) were readily wiped out, and slower growers went to extinction more rapidly than faster growers. Especially when massive mortalities occurred, slower growers were unlikely to reach sexual maturation.

Increases in the strength of both the density-dependent growth γ and the mean of the log-normal distribution of rainfall μ tended to increase the frequency of unimodality, narrow the range of ϕ, and increase both the minimum and maximum values of ϕ at t_{qs} (Table 2; Fig. 7). With the highest μ, the results of CAT were confirmed for either absent or strong density-dependent growth. In Electronic supplementary material 4, we show the main results of simulations performed with different values of γ in scenario CAT and $\mu = 200$ mm.

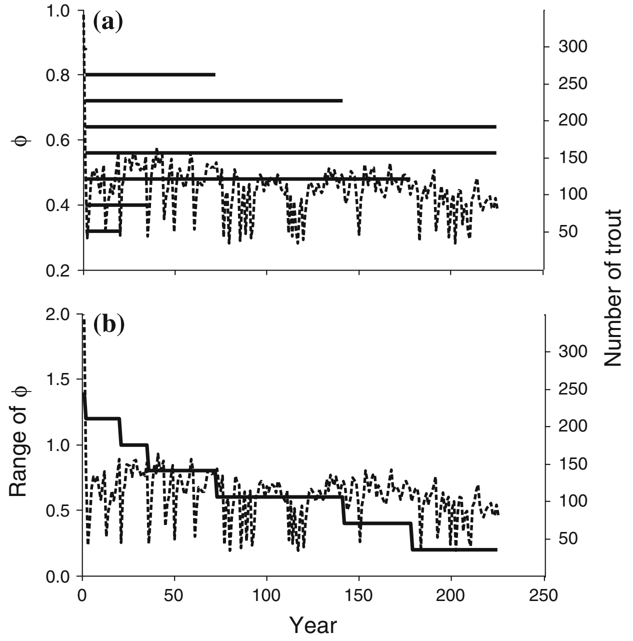

Fig. 6 Example of a replicate with a variable environment and the occurrence of flood events (CAT). In **a**, the *horizontal lines* end when growth parameters in the interval $\phi \pm 0.1$ go to extinction. In **b**, the *continuous solid line* tracks the range of the growth parameter ϕ. In both panels, the *broken line* tracks the number of immature and mature trout (≥age 1) over time

Simulations using different shapes of the initial distribution of growth parameters (uniform, beta and lognormal) and number of individuals in the first year provided essentially the same results, indicating a low sensitivity of the individual-based model of population dynamics to variation in these model parameters. Simulations using different P values of the KS test ranging from 0.5 to 0.8 modified the time t_{qs} needed to reach a quasi-stable distribution by a maximum of 50 years, with a quasi-stable distribution of growth parameters reached more rapidly with lower P values. Widening the range of the uniform distribution of parameter values did not lead to a substantial modification of the simulation results for scenario VAR. Simulations with reduced heritability of ϕ supported the results obtained with perfect inheritance. The main qualitative difference was the presence of a limited

Table 2 Summary of sensitivity analysis

Parameter	Distribution			Range of ϕ_{qs}			Min(ϕ_{qs})			Max(ϕ_{qs})		
	Estimate	Std. error	*P* value	Estimate	Std. error	*P* value	Estimate	Std. error	*P* value	Estimate	Std. error	*P* value
Intercept	2.75	0.68	**	0.14	0.24	°	−0.67	0.07	**	0.18	0.07	**
γ	−1.36	1.30	°	−0.87	0.48	°	0.56	0.13	**	−0.26	0.03	**
μ	−0.011	0.03	**	−0.05	0.001	**	0.003	0.0004	**	−0.00003	0.00009	°

We used generalized linear regression for the response variable Distribution (equal to 1 for bimodality of ϕ_{qs} and 0 for unimodality), and ordinary linear regressions with log-transformed response variables for the range of ϕ_{qs}, min(ϕ_{qs}), and max(ϕ_{qs}). Predictors were strength of density-dependent body growth γ in $L(a|D_U,\gamma,\phi)=\frac{L_\infty}{1+\gamma D_U}\left(1-e^{-k\phi(a-a_o)}\right)$, and mean of the log-normal distribution of autumnal rainfalls μ, with SD = 327. We simulated 50 replicates for each combination of γ and μ, for a total of 1,250 replicates. The interaction between γ and μ was never significant, and thus models were fitted again without the interaction term

* *P* value < 0.05

** *P* value < 0.01

° *P* value > 0.05

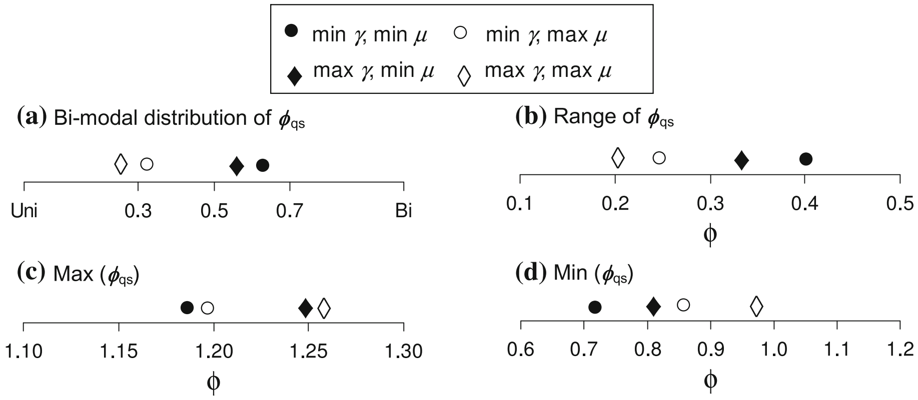

Fig. 7 **a** Proportion of the distribution of ϕ_{qs} that is bimodal, **b** range of ϕ_{qs}, **c** max (ϕ_{qs}), and **d** min(ϕ_{qs}) obtained by applying the regression models of the sensitivity analysis for a combination of maximum ($\mu = 300$, $\gamma = 0$) and minimum ($\mu = 200$, $\gamma = 0.2$) values of strength of density-dependent growth (γ) and the mean of the log-normal distribution of autumnal rainfalls (μ)

number of very fast growers in CAT replicates (see Electronic supplementary material 2).

Discussion

Episodes of massive mortality may trigger a chain of impacts directing the selection of a limited range of intermediate growth parameters in the population. Severe floods greatly reduce the size of a population by flushing away or killing individuals, and the resulting relaxation of density-dependent pressure allows fish to rapidly increase in body size. Although some within-population variations in morphological and behavioral adaptations to floods may occur (Lytle 2000; Ward et al. 2003; Lytle and Poffs 2004), random deaths of fish are a reasonable assumption in the case of severe flash floods or debris flows. In the years immediately following the episode of massive mortality, fast-growing fish (those with ϕ slightly greater than 1) can reach maturity faster, and—given the positive relationship between body length of females and fecundity—produce more eggs than slow-growing fish. It is worth noting that the growth parameter distributions that were likely to be found at the end of simulations in the scenario with catastrophes (CAT) were in the neighborhood of the "base case," which may suggest that flood events are major contributors to growth rate selection in marble trout.

Across taxa, it is common for selection to favor larger body size, as larger individuals are more likely to have a higher survival, greater fecundity and greater mating success (Kingsolver and Pfennig 2007). Kingsolver and Diamond (2011) explored the potential of fitness trade-offs, indirect selection, and fluctuating selection to constrain or limit overall directional selection. For body size, they suggest that negative indirect selection due to correlated traits (phenology, development time, mortality) could reduce the total net sized-based selection (Lande 1976). The view that trait evolution is restricted or biased by fitness trade-offs is widely supported (Roff 2002); in this case, a trade-off occurs when a potential increase in fitness due to a change in one trait is opposed by a decrease in fitness due to a concomitant change in the second trait. Therefore, under a particular set of selective forces, specific combinations of traits will be favored in a given population within the particular physiological and genotypic constraints of the considered species. Mangel and Stamps (2001) investigated the fitness consequences of growth–mortality trade-offs in fish populations using a simple life-history model with parameter values approximating the life histories of brown trout (*Salmo trutta* L.) or Arctic charr (*Salvelinus alpinus*) and no environmental variability. They found that a variety of different growth parameters produce virtually the same fitness, where fitness was defined as the solution of the Lotka–Volterra equation. While the authors encouraged further thoughts on "whether a value $r = 0.110$ really differs from $r = 0.111$," they argued that the near-equivalent fitness induced by a variety of growth rates may promote the coexistence of individuals with relatively large differences in growth rates within the same populations. They found that very fast and very slow growers had lower fitnesses than individuals with intermediate values of the growth parameter.

In our simulations, we observed strong selection against very fast and very slow growers in all three scenarios. Mutants with growth parameters ϕ that approached the boundaries of the distribution ($\phi \rightarrow 2$ and $\phi \rightarrow 0$) rapidly went extinct. This is consistent with observations of selection against very fast and very slow growers (Wootton 1998a, b). Temporal fluctuations in selection could also alter the consequences of directional selection (Siepielski et al. 2009). Kingsolver and Diamond (2011) noted that the key issue is whether such temporal fluctuations are sufficient to reduce the cumulative effects of directional selection over time (Bell 2010), presumably leading to individuals with an intermediate growth phenotype having the highest fitness (Travis 1989), even when faster growers would theoretically be favored. The most likely explanation for the occurrence of very fast growers in the catastrophic scenario with reduced heritability is the generation of a limited number of individuals with very fast growth due to mutation–segregation–recombination.

Our results showed that primarily flood events, and not density-dependent processes, are driving the exclusion of slower growers from the population. The loss of slow growth traits over time could be considered a local adaptation to the occurrence of high-amplitude stochastic events. Gutschick and BassiriRad (2003) proposed that selection on plant physiology is strongest during the prolonged recovery phase after an extreme event, and that the traits of resource acquisition and usage efficiency drive plant performance during the recovery after the impact of an extreme event. An interesting parallel can thus be made with our system, where slower growers are outcompeted by faster growers during the recovery phase after the flood event. Other studies have shown that different growth rates and growth trajectories are selected by different environments. In an experiment with coho salmon, Sundström et al. (2005) found that environmental conditions substantially modulated the relative effect of intrinsic growth rate in fast-growing transgenic individuals, indicating that strong genotype-by-environment interaction effects were influencing the fitnesses of the genotypes. Using numerical experiments, Gurney and Middleton (1996) found different selections on body growth in constant and variable environments. No growth after sexual maturity (determinate growth) was the optimal strategy in both constant and weakly variable environments. A significant change in optimal strategy was observed in an intensely varying environment, with growth after maturity (indeterminate growth) favored over wide ranges of individual and environmental parameters. They also found that for a shift toward growth to occur after maturity, there must be a significant probability that there are years in which the resource supply is small enough to drive the population to very low levels.

In the case of absence of flood events, the bimodal distribution of growth parameters in the population in the vast majority of replicates might suggest the operation of disruptive selection on individual growth rates. Elliott (1989) found a high coefficient of variation in length in year-two classes of two populations of brown trout growing in a laboratory, associated with the development of three distinct modes in the size–frequency distribution. Glover et al. (2003) monitored the growth of three pure stocks and one hybrid stock of anadromous brown trout under controlled conditions from hatching for a period of 16 months. Two of the stocks developed clear bimodal length–frequency distributions, whereas the other two stocks displayed skewed or weakly bimodal length–frequency distributions. Vincenzi et al. (2007b) did not observe polymodality in the length–frequency distribution of marble trout, and our analysis suggests that episodes of massive mortality may contribute to the observed pattern, since all marble trout populations living in Slovenian streams are impacted by flood events. We predict that in populations which are adapted to stream environments that are not subject to flood events, multi-modality of the length–frequency distribution may be observed.

It is clear that the effects of extreme events on the evolutionary dynamics of fish can be substantially different to those driven by stochastic—but not catastrophic—environments. The impact of extreme flood events on stream-dwelling salmonids is likely to increase as a consequence of ongoing climate change. According to IPCC projections, the frequency of extreme flood events is expected to increase in the next 50 years (Solomon et al. 2007), and recent studies seem to support the IPCC projections (Min et al. 2011; Pall et al. 2011). This suggests that the consequences of flood events for population dynamics and the life histories of freshwater fish deserve further and wider explorations in the context of eco-evolutionary dynamics (Pelletier et al. 2009).

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