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Genetic and life-history consequences of extreme climate events

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Climate change is predicted to increase the frequency and intensity of extreme climate events. Tests on empirical data of theory-based predictions on the consequences of extreme climate events are thus necessary to understand the adaptive potential of species and the overarching risks associated with all aspects of climate change. We tested predictions on the genetic and life-history consequences of extreme climate events in two populations of marble trout *Salmo marmoratus* that have experienced severe demographic bottlenecks due to flash floods. We combined long-term field and genotyping data with pedigree reconstruction in a theory-based framework. Our results show that after flash floods, reproduction occurred at a younger age in one population. In both populations, we found the highest reproductive variance in the first cohort born after the floods due to a combination of fewer parents and higher early survival of offspring. A small number of parents allowed for demographic recovery after the floods, but the genetic bottleneck further reduced genetic diversity in both populations. Our results also elucidate some of the mechanisms responsible for a greater prevalence of faster life histories after the extreme event.

1. Introduction

Empirical and theoretical research on the demographic, genetic and life-history effects of a changing climate (e.g. changes in population size and spatial distribution, age structure, genetic variability, growth, age at maturity) has mostly focused on trends in the means of climate variables, such as temperature or rainfall, over seasons or years. These effects are reasonably well understood across species over various time scales [1,2]. For instance, interspecific and spatial variation in population abundance of birds were well predicted on a global scale by climate suitability trends, confirming that theoretical expectations about how a species responds to climate change can predict actual responses [3].

One generally under-appreciated effect of climate change is the increase in the frequency and intensity of extreme climate events [4], which range from local events such as tornadoes and flash floods to climate-scale events, such as droughts, that can develop over weeks or months [5]. Tests of theory-based predictions on the consequences of extreme events with empirical data are scarce, though necessary and urgent to provide a balanced view of the adaptive potential of species and the overarching risks associated with all aspects of climate change [6–8]. However, when dealing with extreme events, finding the right model system, posing and testing tractable hypotheses on their demographic, genetic and life-history consequences, and developing an overarching predictive framework are inevitably challenging [8].

The first challenge is that climate extremes that result in strong demographic and genetic responses are, by definition, rare events. As a result, most of the empirical studies on the effect of extreme events have been opportunistic and anecdotal; for instance, limited information on the study system before the occurrence of the extreme climate event does not typically allow before–after comparisons [8]. Furthermore, the demographic and genetic effects of climate extremes, such as population crashes, loss of genetic diversity, inbreeding and maladaptation [9], changes in population age and size structure [10], and shifts in phenology [11], are often the result of chance and specific to the life histories of the organisms studied, and are thus not easily predictable or generalizable across species or habitats.

However, a few general predictions about the demographic, genetic and life-history consequences of extreme events have been formulated, with varying support from empirical studies [12]. First, extreme events directly increase the risk of extinction by inducing massive mortalities [13]. In some cases, extreme events may be so severe that extirpation is inevitable in the absence of immigration.

Second, additive genetic variance, allelic diversity and polymorphism are predicted to decrease in populations that experience bottlenecks [14]. As adaptive potential theoretically increases with genetic variability, and genetic drift may overwhelm selection in small populations [15], lower genetic variability is predicted to increase both short- and long-term risks of population extinction [16].

Third, life-history theory [17] predicts selection for opportunistic, faster life histories in populations that are affected by periodic events that strongly reduce adult population size [18]. Such responses have been found in studies of fishery-induced evolution: since harvesting increases adult mortality, there are fewer benefits to delaying reproduction [19].

Faster life histories are characterized by accelerated growth early in life, younger age at reproduction and higher reproductive effort (i.e. more energy allocated to reproduction at the expense of survival). They tend to provide higher population growth rates than older age at maturity and lower reproductive effort [20], thus increasing the chances of population recovery after a drastic reduction in adult population size. The greater prevalence of faster life histories after extreme events may be transient and be partially determined by more resources available *per capita* for growth and lower competition for mates for younger individuals. With a greater prevalence of faster life histories, population age and size structure are also predicted to change, often in the direction of younger and relatively smaller (especially at older ages) individuals.

In the case of extreme events that are seasonal and predictable, life-history theory also predicts shifts in the phenology of plant and animal species, as has been found in experiments with grassland and heath species [11], as well as in caddisflies living in streams affected by flash floods [21]. Variance in reproductive success is also predicted to increase after extreme events, with number of parents per offspring predicted to be at its lowest in the first year class (offspring) after the extreme event due to a combination of fewer parents and increased survival of offspring in the first few years post-extreme event, due to lower competition.

Here, we used long-term tag–recapture data and genetic parentage analysis [22,23] to test theory-based hypotheses on

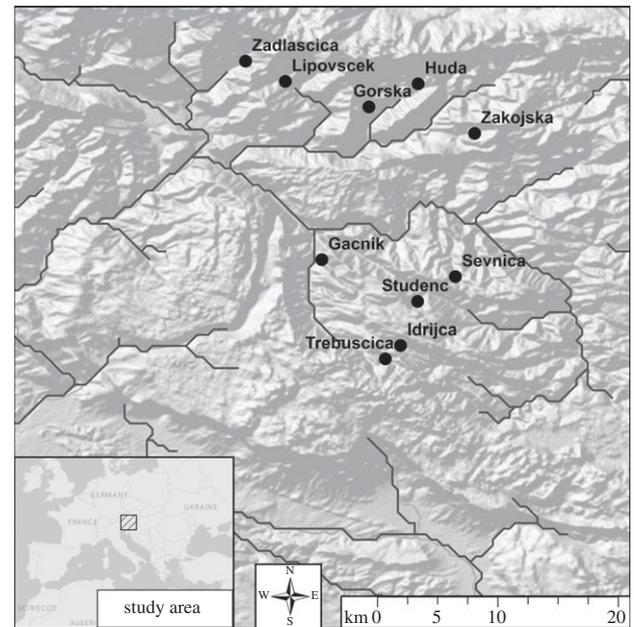


Figure 1. Location of streams in western Slovenia in which remnant (Zadlascica, Lipovscek, Huda, Sevnica, Studenc, Trebuscica and Idrija) and newly created (Zakojska and Gacnik) populations of marble trout live. The population living in the Gorska stream was extirpated by a flash flood in 2004.

the genetic and life-history consequences of flash floods affecting populations of marble trout *Salmo marmoratus* (Cuvier), a freshwater salmonid species endemic to rivers tributary to the upper Adriatic Sea. Marble trout are of great conservation concern, as they persist in non-introgressed form in small, isolated populations in western Slovenia and northern Italy [24] and face growing threats from climate change in the form of increased water temperature and frequency and intensity of flash floods.

We focused on the marble trout populations of Zakojska and Lipovscek (figure 1), which have been the subject of intensive monitoring since 1996 (Zakojska) and 1999 (Lipovscek). These two populations experienced flash floods in 2007 (Lipovscek and Zakojska), and 2009 (Lipovscek) that caused habitat destruction and mortality or displacement of a large fraction of the population, with survival rates 90% lower than survival rates in non-flood years [25]. In the years following the floods, there was a substantial increase in early survival and growth of fish in both populations, mostly due to relaxation of the effects of density on vital rates [25], which contributed to a partial recovery in both populations, albeit at lower population densities.

We genotyped approximately 1800 marble trout from the populations of Lipovscek and Zakojska using single-nucleotide polymorphisms (SNPs) and reconstructed pedigrees to test predictions of the effects of extreme climate events on genetic variability and life histories of the affected species. In particular, we tested for (i) younger age of parents after floods, (ii) lower numbers of parents per offspring in the first year class after floods, (iii) increase in the proportion of fixed alleles (i.e. fewer polymorphic loci) in the year-classes born after floods, and (iv) decrease in mean heterozygosity across individuals born after floods.

2. Material and methods

(a) Species and monitored populations

Marble trout is a freshwater salmonid fish of great conservation concern, due to its restricted geographical distribution and the risk of hybridization with alien brown trout (*Salmo trutta* L.). Only eight natural and two re-introduced populations of genetically pure marble trout remain (figure 1), all in streams in the river basins of Soča, Bača and Idrija in Slovenia [26], persisting above barriers that have prevented the upstream movement of brown trout or of marble-brown trout hybrids [24]. Marble trout spawn in November–December and offspring emerge in May–June. As such, for example, eggs of cohort 2011 were produced in November–December of 2010 and fish emerged in May–June 2011. Marble trout females typically reproduce at age 3+ and older, and at a minimum size of 200 mm, and males age 2+ and older [27].

The population of Zakojska (Zak; lat: 46.1699522 N; long: 13.9510114 E) was established in 1996 by introducing 500 age-1 fish raised in captivity that descended from the genetically pure population of Zadlascica (figure 1). Natural production first occurred in this formerly fishless stream in 1998. The population of Lipovscek (Lipo; lat: 46.2091274 N; long: 13.809643 E) is a relict pure population. Both streams are located in remote locations without any regulated fishing, known poaching or the presence of predators or other fish species.

The population of Zak was sampled once a year in June, while the population of Lipo was sampled bi-annually in June and in September. Tagging and collection of genetic samples started in 1996 in Zak and in 2006 in Lipo, although population density was estimated in Lipo starting in 1999. The entire population of Lipo inhabits a 1040 m stretch of habitat, constituted by upstream (LipoU) and downstream (LipoD) sub-populations occupying habitat of approximately equal length and separated by a waterfall that almost completely prevents upstream movement of fish from LipoD to LipoU (electronic supplementary material, figure S1). For most years and cohorts, all analyses are for LipoD. Between 1999 and 2005, fish were sampled (but not tagged) in two non-contiguous stations in LipoD to estimate density. In 2006, fish were tagged in one of the two sampling stations, and in the other fish were sampled (but not tagged) to more accurately estimate density. In 2007 and in the following years, due to a substantial decrease in fish numbers caused by the flood, fish were tagged (and sampled) in all of LipoD. Fish have never been tagged in LipoU, but genetic samples were collected in LipoU in September 2008 and September 2011 to gain a more complete picture of the process of recovery or extinction after the 2007 and 2009 flash floods. Thus, for cohort 2011 only (the first of sizable dimension born after the floods of 2007 and 2009) we consider both LipoD and LipoU. Habitat encompassing the entire population of Zak (approx. 1230 m long) has been sampled every year since 1996. Zak is a fragmented stream in which upstream movement of fish is severely limited due to the presence of waterfalls.

Fish were captured by electrofishing and netting. If a fish was caught for the first time or if the tag had been lost, and the fish was longer than 110 mm, it received a Carlin tag and age was estimated by reading scales. The adipose fin was removed on each fish not previously tagged, both for identification as a previously tagged fish and as a genetic sample. Sub-yearling fish are termed 0+ and are too small to be sampled and handled in June, thus we were only able to sample them in Lipo in September.

Sub-yearlings are smaller than 110 mm in both June and September, so tagging began at age 1+ or, for slow-growing fish, at age 2+. Sex was assigned using a molecular genetic assay developed for marble trout using the sequence information described in [28]. The movement of marble trout is very limited, and the majority of fish were sampled within the same 50–100 m

stream reach throughout their lifetime [29]. The oldest fish sampled in Lipo and Zak were 8 and 12 years old, respectively. In our analyses involving tagged fish, we included samples and data collected between June 1996 and June 2013 for Zak, and between June 2006 and September 2014 for Lipo.

(b) Floods

Major autumnal floods (often in the form of flash floods) in western Slovenia have been recorded since the eighteenth century, recurring approximately every 50 years [30]. A substantial increase in the frequency of autumnal floods has been observed in recent years, and since 2009 spring floods have also been recorded [31]. Since 1993, when intensive monitoring of the marble trout populations began, major autumnal floods and debris flows have greatly reduced population size and caused substantial habitat destruction in the populations of Lipo, Zak, Sevnica and Zadlascica (figure 1). The population of Predelica was extirpated by a landslide triggered by intense rainfall in 2000 [25].

(c) Density

We estimated density of fish by age, size class or cohort using a two-pass removal protocol [32] as implemented in the R [33] package FSA [34]. We estimated density of 0+ fish only in LipoD in September. Stream surface area (m²) was used for the estimation of fish density (in fish ha⁻¹). In LipoD, the same two, non-contiguous sampling stations were used to estimate density between 1999 and 2014.

(d) SNP genotyping

DNA extracted from fin clips was diluted 2 : 1 with distilled water and used for polymerase chain reaction amplification of 118 SNPs for Lipo and 94 SNPs for Zak (electronic supplementary material, Text S1). SNPs were assayed with 96.96 genotyping IFC chips on an EP1 (EndPoint Reader 1) instrument (Fluidigm). Genotypes were called using SNP genotyping analysis software (Fluidigm). All genotypes were called independently by two people, and discrepancies in the scores were resolved by consensus, by re-genotyping, or by deletion of that genotype from that dataset. A proportion of individuals were genotyped more than once (approx. 20% of individuals in Lipo and approx. 15% in Zak), as determined by observed identical genetic profiles and compatible age and length data; in those cases, one of the genotypes was excluded from further analyses. Mean \pm s.d. minor allele frequency (MAF) of the SNPs was 0.23 ± 0.15 for Lipo (electronic supplementary material, table S1) and 0.28 ± 0.13 for Zak (electronic supplementary material, table S2). Such MAFs with nearly 100 or more SNPs are sufficient for parent-pair/offspring trio reconstruction with high accuracy [35]. The final dataset included 550 (Lipo) and 1289 (Zak) genotyped individuals that were identified either as offspring or potential parents and used in the analyses in this study.

(e) Pedigree reconstruction and age at spawning

We used a conservative, two-step approach for reconstructing pedigrees. We first inferred mother–father–offspring trios using the software SNPPIT [22], and then used the software FRANz [23] to validate trios and infer single parent–offspring pairs. Further details on pedigree reconstruction are in the electronic supplementary material, text S1.

For both Lipo and Zak, the first cohort of sizable dimension (more than 20 fish) born after the floods was the one born in 2011. Differences in mean age at reproduction for the first cohorts produced by parents born after the floods (2013 and 2014 in Lipo, 2013 in Zak) and all the previous generations pooled together were tested with *t*-tests. To test for changes in reproductive output after the floods, we calculated the mean number of parents-per-offspring for each cohort, which is obtained by dividing the total

number of parents by the total number of offspring in the cohort produced by those parents. For cases in which only a single parent of an offspring was identified, we assumed that it mated with a single, unique, unidentified parent. Parents per offspring has an upper bound of 2 (each offspring produced by a different parent pair) and a lower bound with limit of 0.

(f) Heterozygosity and loss of alleles

We calculated heterozygosity at the individual level as the proportion of heterozygous loci and tested whether flood-induced mortality events changed mean heterozygosity using *t*-tests. We estimated the loss of alleles as difference between cohorts in the proportion of fixed (i.e. monomorphic) loci. Owing to unequal sample size, we carried out jackknife rarefaction calculations using ad-hoc algorithms in R.

3. Results

(a) Effects of floods on density

The flash floods that occurred in Zak and Lipo on 19 September 2007 were caused by the highest daily rainfall recorded in both basins between 1996 and 2013 (approx. 220 mm in Zak and approx. 300 mm in Lipo; electronic supplementary material, figures S2 and S3). The flood that occurred on 25 December 2009 in Lipo was caused by approximately 227 mm of rainfall in a single day (electronic supplementary material, figure S3), which was substantially higher than the average of annual maximum daily rainfall over 1996–2013 (177 mm).

The number of fish sampled in LipoD ranged from 3 (September 2010) to 175 (September 2012) and in Zak from 11 (June 2008) to 396 (June 2002). A partial population recovery was evident after the 2007 flood in both LipoD and Zak, albeit at lower population densities than those recorded before the event (figure 2). There were almost complete reproductive failures in 2008 and 2009 in Lipo and in 2009 and 2010 in Zak. In Lipo (LipoU and LipoD), 332 fish born in 2011 were sampled at least once at age older than 0+. Also in Zak, the first sizable post-flood cohort in Zak was in 2011, with 87 fish that were sampled at least once at age older than 0+. After the flood and before the production of cohort 2011, all the surviving fish in Zak were either located in an approximate 150 m stretch close to the uppermost part of the stream or in a downstream section separated by the rest of the stream by an impassable waterfall.

(b) Pedigree reconstruction and reproduction

(i) Assignment of progeny to parents

We obtained a good reconstruction of pedigrees in both Zak and Lipo. In Zak, 61% of genotyped samples were assigned to parent-pairs, 11% to single parents and 28% were not assigned (electronic supplementary material, figure S4). In Lipo, 36% of genotyped samples were assigned to parent-pairs, 31% to single parents and 33% were not assigned (electronic supplementary material, figure S5). In Zak, the median age at spawning over all years was 4 for both males and females (electronic supplementary material, figure S6), while in Lipo it was two for both males and females (electronic supplementary material, figure S7).

(ii) Reproduction after floods

Zak. A few parents produced a large part of the post-flood cohorts. The 2011 cohort of Zak was almost entirely (76 out of 83 fish assigned to parents) produced by two parents born in

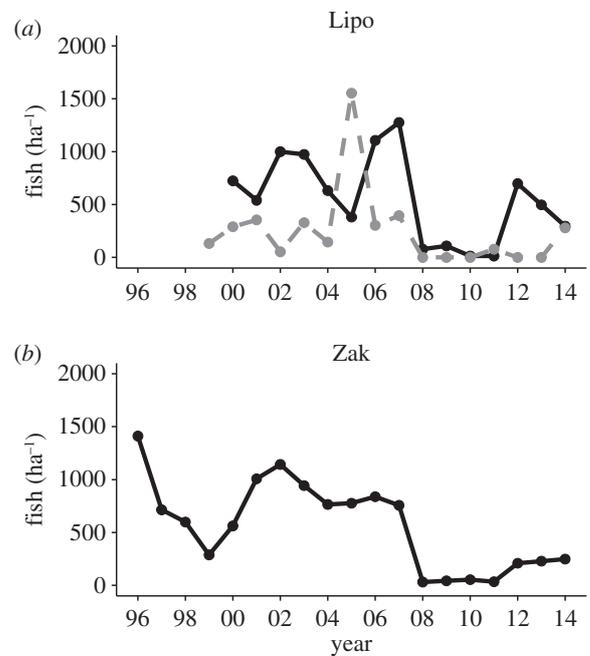


Figure 2. Density over time of marble trout in age classes 0+ (dashed line) and more than 0+ (solid line) in September for Lipo and in June (only older than 0+) in Zak. Severe flash floods and debris flows occurred in Lipo in 2007 and 2009, and in Zak in 2007. Estimation of density started in 1999 in LipoD and in 1996 in Zak.

2004 and 2007. The parent born in 2007 also produced 12 out of 17 assigned fish of the 2012 cohort and four out of six assigned fish of the 2013 cohort. Four out of six offspring of the cohort 2013 were the progeny of a male aged 1+. Most of the other fish from previous cohorts produced by parents aged 1+ (44 out of 56) were produced by parents born between 1998 and 2001, when population density was very low (figure 2). In total, 11 females and 16 males reproduced at age 1+.

Lipo. Six highly productive parents produced most of the 2011 cohort, but no offspring born in 2013 and 2014 were assigned to any of those parents. Nearly 60% of the 220 assigned fish from the 2011 cohort were the progeny of two parent pairs; 46 were offspring of a parent pair living in LipoD (age 3+ and age 6+ at the time of spawning) and 84 of a parent-pair living in LipoU (both age 4+). Approximately 37% of the assigned fish from the 2011 cohort were the progeny of two identified single parents, one living in LipoU and the other in LipoD at the time of spawning.

Approximately 65% (21 out of 33) of the assigned offspring of the 2013 cohort were the progeny of a single parent pair (age 2+ female and age 1+ male). Another female and another male, both aged 1+, produced 1 and 2 offspring of the 2013 cohort, respectively. Twenty-one of the 33 assigned offspring of the 2014 cohort were the progeny of two parent pairs, each with parents of age 3+ and 2+ (neither of those parents produced sampled progeny in earlier years). For all cohorts older than the 2013, a total of 20 offspring were assigned to nine different parents aged 1+, six of which were born between 2003 and 2005, when population density was low (figure 2). In total, five females and eight males were found to have spawned at age 1+.

Age of parents born before and after the floods, and parents per offspring. In Zak, the small number of parents of the sole post-flood cohort, 2013 (mean \pm s.d., years: 3.50 ± 1.73 , $n = 4$), precluded a statistical test of differences in mean age at spawning with parents of previous cohorts (3.82 ± 1.85 ,

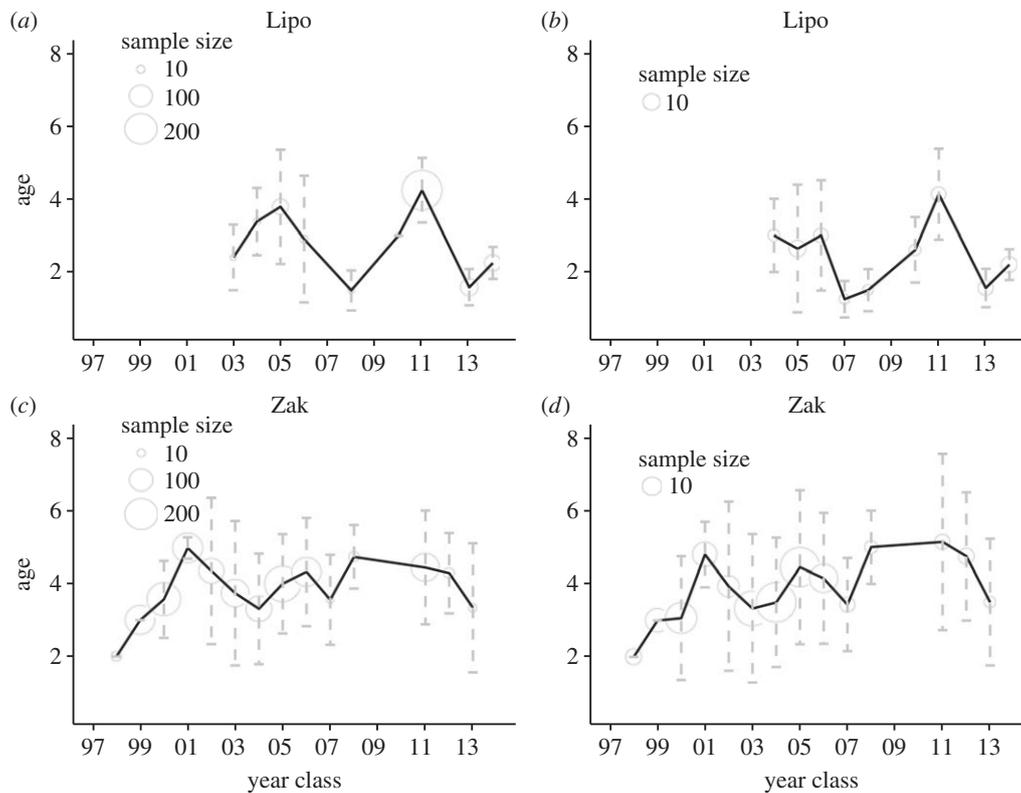


Figure 3. (a,c) Mean \pm s.d. of age of parents for each cohort in (a) Lipo and (c) Zak when considering both parent pairs and single parents, and each parent enters the calculation n times when n is the number of offspring. Sample size is the number of offspring assigned. (b,d) Mean \pm s.d. of age of parents for each cohort in (b) Lipo and (d) Zak when considering both parent pairs and single parents, and each parent enters the calculation once. Sample size is the number of unique (identified) parents.

$n = 298$; figure 3d). Parents of the 2013 and 2014 cohorts in Lipo were significantly younger (mean \pm s.d.: 1.89 ± 0.56 , $n = 19$) than parents of earlier cohorts (2.70 ± 1.47 , $n = 49$; t -test, %95 CI = [0.30–1.29], $p < 0.01$; figure 3b).

Parents per offspring was at its minimum for the first cohort of appreciable size born after the flash floods in Zak and Lipo (cohort 2011), due to a combination of fewer parents and high production of offspring (figure 4).

(c) Heterozygosity and loss of alleles

Mean heterozygosity (figure 5) and proportion of fixed alleles (figure 6) changed through time in both Lipo and Zak.

In Zak, heterozygosity was lower ($p < 0.01$) in fish born after the 2007 flood than in fish born before the flood (mean \pm s.d. proportion of heterozygous loci, before flood: 0.37 ± 0.08 , $n = 1163$; after: 0.34 ± 0.06 , $n = 121$; figure 5b). Heterozygosity tended to decline more rapidly in cohorts born after 2011 (electronic supplementary material, text S2). On the other hand, the proportion of fixed alleles was higher ($p < 0.01$) in cohorts born after the 2007 flood (figure 6b). Also in Lipo, heterozygosity was lower ($p < 0.01$) in fish born after the 2007 flood than in fish born before the flood (mean \pm s.d. proportion of heterozygous loci, before flood: 0.35 ± 0.10 , $n = 156$; after: 0.32 ± 0.06 , $n = 394$), but it increased in the last cohort sampled (figure 5a). The proportion of fixed alleles was higher ($p < 0.01$) in cohorts born after the 2007 flood (figure 6a).

4. Discussion

A robust understanding of the effects of extreme events on demography, population dynamics, life histories and risk of

extinction of natural populations is critical for population forecasting and managing human intervention in a changing world.

Our results show that flash floods that caused massive mortalities in two marble trout populations led to (i) a decrease in mean age in reproduction after the floods in one of the two populations (Lipovscek), and in both populations (ii) a decrease in the number of parents-per-offspring for the first cohort born after the floods, (iii) an increase in the proportion of fixed alleles in cohorts born after the floods, and (iv) lower mean heterozygosity for individuals born after the floods.

(a) Reproduction after extreme events and evolution of life histories

In salmonids, only a small fraction of potential spawners achieve reproductive success in most years so that the productivity of successful spawners is highly skewed [36]. Consistent with this and the higher post-flood early survival, we observed the lowest parents per offspring ratio for the first large cohort born after the flash floods in both populations.

Flash floods and debris flows such as those occurring in western Slovenia are unlikely to directly select for particular phenotypes (e.g. morphology, avoidance behaviour and reproductive traits) through differential survival [18], owing to their catastrophic effects (i.e. with survival rates 90% lower than survival rates in non-flood years) and relative rare occurrence. Life-history theory predicts that infrequent or temporally unpredictable disturbances should have little effect on the evolution of life-history strategies such as size at and timing of maturity or avoidance behaviour [37]. In the case of flash floods and debris flows affecting marble trout, survival of fish is thus expected to be largely determined by chance; for

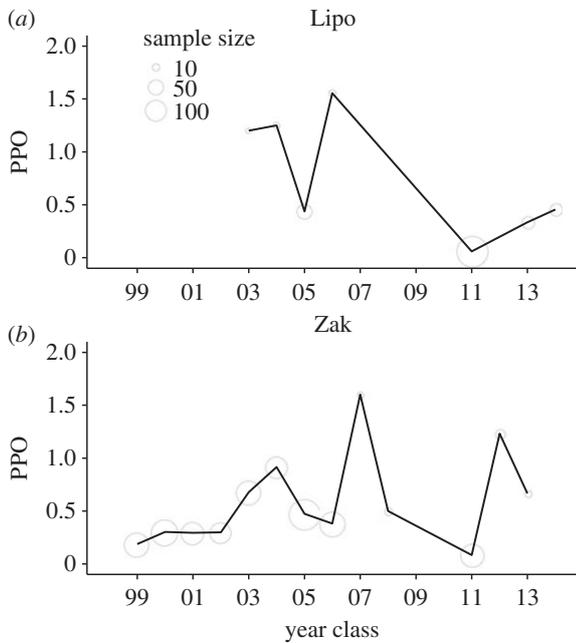


Figure 4. Number of parents per offspring (PPO) in each cohort in (a) Lipo and (b) Zak. Sample size is the number of fish assigned to single parents or parent pairs in each cohort.

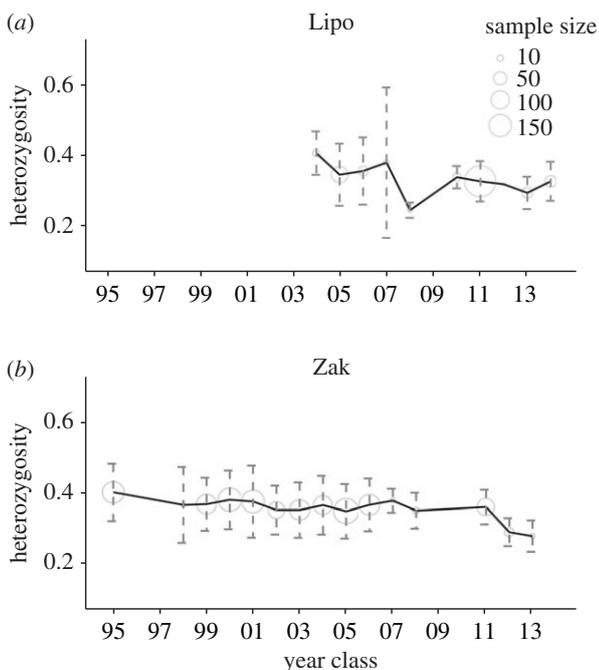


Figure 5. Mean and standard deviation of individual heterozygosity across fish in each cohort in (a) Lipo and (b) Zak. Individual heterozygosity was calculated as the proportion of heterozygous loci. Sample size is the number of genotyped fish in each cohort.

instance, in Zakojska the only fish surviving the 2007 flood (along with some individuals displaced downstream) were living in the uppermost part of stream, which was probably less affected by fast waters and debris.

However, the conditions created by such extreme events in the years following their occurrence (e.g. greater *per capita* resources such as food and space due to transient low population density and mobilization of nutrients, fewer older fish) may increase the prevalence of more opportunistic life histories through selection, phenotypic plasticity or changes in population age and size structure [18,29].

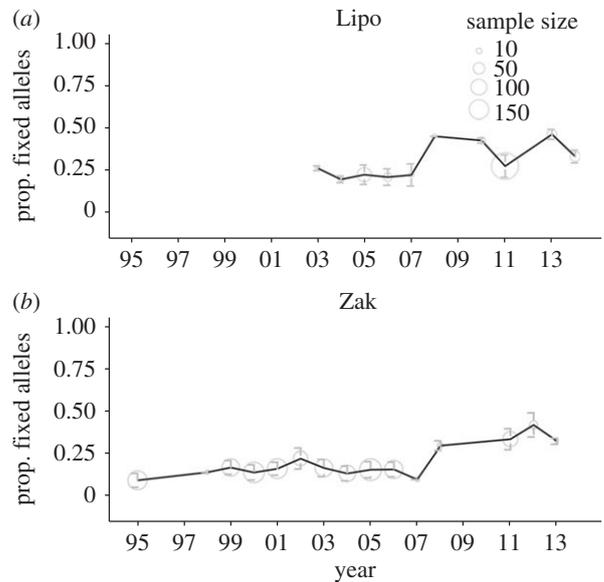


Figure 6. Mean proportion of fixed alleles (118 loci in Lipo and 94 in Zak) in each cohort \pm s.d. across replicates for cohorts with at least five individuals genotyped in (a) Lipo and (b) Zak. Sample is the number of fish genotyped in each cohort. Jackknife rarefaction was carried out with sample size equal to 5, which is the minimum sample size across cohort.

Both the increase in somatic growth rates [25] and the younger mean age at reproduction (this study) indicate a short-term prevalence of faster life histories in Lipovscek following an episode of massive mortality. Both growth and reproductive traits are heritable [38], and can thus respond adaptively to changes in the fitness landscape. Rapid growth and younger age at reproduction are opportunistic strategies usually found under conditions that increase adult mortality [19], and should increase fitness in populations subject to boom-and-bust cycles. However, younger age at reproduction can also be a consequence of faster growth—which is mostly caused by lower population density and fewer older fish occupying profitable stream habitat—when sexual maturation is size-dependent (as in the case of salmonids) and/or fewer older fish competing for mates. As we observed in this study, some marble trout can be sexually mature when very young (e.g. at age 1+) also in normal (i.e. not following extreme events) conditions, but they may be more likely to successfully reproduce when fewer older fish compete for mates. Vincenzi *et al.* [29,39] found in theoretical work that faster growth due to lower density and younger age at reproduction due to size-dependent sexual maturity—or weaker competition for mates—should increase the probability of persistence of marble trout populations affected by extreme events.

The question is whether the prevalence of faster life histories observed in Lipovscek after the flash flood will be maintained over longer time frames, or whether higher population density and a greater number of older fish competing for space, food and mates would reduce average growth and increase mean age at reproduction. Given that younger parents were in both populations more frequent in years with low population density, and following the theoretical results of Vincenzi *et al.* [18], our hypothesis is that faster growth and younger age at reproduction observed in Lipovscek after the flash floods are more likely to be a transient response, mostly determined by lower density, more (or better) food and space available after the extreme events, and fewer older fish competing for mates [40,41].

Vincenzi *et al.* [18] showed that when the interval between extreme events is longer than a species's generation time, changes to the fitness landscape at higher population densities are expected to favour slower-growing, longer-living phenotypes [18], thus acting against any selection for faster life histories occurring in the first few years following the extreme events. Similarly, in harvested species, a sudden reduction in adult mortality (e.g. a ban on harvesting) favours the evolution of slower life histories characterized by delayed maturity and large adult body size [19]. However, since the recurrence interval of flash floods in Slovenian streams is expected to decrease and approach the generation time of marble trout [42], it is possible that faster life histories in marble trout will become more steadily prevalent in the future, and not be simply transient occurrences [18]. A few additional years of demographic and genetic data will allow us to test whether the observed shift to younger age of parents after the extreme events would be maintained.

The lower median age at spawning we observed in Lipovscek is consistent with the findings of Vincenzi *et al.* [25] on the position of Lipovscek and Zakojska in the fast-to-slow life-history continuum of marble trout populations—Lipovscek characterized by faster growth rates and intermediate survival, and Zakojska by slower growth rates and high survival. Differences in the pace of living between populations may have implications for their probability of persistence: populations with slower life histories may be at greater risk of extirpation than those with faster ones, as faster growth and younger age at reproduction should more rapidly increase population size after floods and other events causing massive mortality [29]. It is tempting to hypothesize a relationship between faster life histories in Lipovscek than in Zakojska and frequency of floods, but sample size is small, and other hypotheses, such as different trophic conditions in the two streams leading to differences in life histories, may have more support [25].

(b) Heterozygosity and loss of alleles

In both marble trout populations, the bottlenecks caused by the floods increased the proportion of fixed alleles and decreased heterozygosity in the cohorts born after the extreme events. The effects of floods on heterozygosity and loss of alleles were more pronounced in Zakojska, in which a smaller number of parents heavily contributed to the post-flood cohorts, and reproductive success was even more skewed than in Lipovscek. The loss of within-population genetic diversity induced by extreme events is a major risk factor for the

long-term persistence of marble trout populations, which have already experienced extreme genetic drift and have very low within-population genetic diversity [26]. Loss of genetic diversity and inbreeding are unavoidable in small and closed populations, and it is well known that consequent inbreeding depression can increase the population risk of extinction [15]. In contrast to this, the marble trout population of Huda—which is the most inbred of the remaining genetically pure populations (average $F_{IS} \sim 0.8$; S.V. 2016, unpublished data)—has the population with the highest average survival and has persisted as a small and isolated population for at least a few decades, and probably for centuries [25].

However, the existence of a clear, directional relationship between population size and adaptive potential is controversial. Laboratory studies have often found a positive relationship between population size and either quantitative genetic variation or response to selection [43,44], but a recent meta-analysis on 172 populations of 80 species found that genetic drift does not weaken adaptive potential or trait heritability in small populations [45]. Although this may suggest that marble trout population are not at imminent risk of extinction due to the effects of low genetic variability, further loss of diversity after extreme events in these populations may contribute to the risk of extinction due to low evolutionary potential.

Ethics. All sampling work was approved by the Ministry of Agriculture, Forestry and Food of Republic of Slovenia and the Fisheries Research Institute of Slovenia. Sampling was supervised by the Tolmin Angling Association (Slovenia).

Data accessibility. Tag–recapture SNP-genotypes datasets for Zakojska and Lipovscek marble trout populations: <http://dx.doi.org/10.5061/dryad.f4s16> [46].

Authors' contributions. S.V., A.J.C., M.M. and J.C.G. conceived the ideas and designed methodology; A.J.C. and D.J. collected the data; S.V. and J.C.G. analysed the data; S.V., J.C.G., M.M. and A.J.C. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests. We declare we have no competing interests.

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