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Research

Rapid evolution of thermal plasticity in mountain lake *Daphnia* populations

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Populations at risk of extinction due to climate change may be rescued by adaptive evolution or plasticity. Selective agents, such as introduced predators, may enhance or constrain plastic or adaptive responses to temperature. We tested responses of *Daphnia* to temperature by collecting populations from lakes across an elevational gradient in the presence and absence of fish predators (long-term selection). We subsequently grew these populations at two elevations in field mesocosms over two years (short-term selection), followed by a common-garden experiment at two temperatures in the lab to measure life-history traits. Both long-term and short-term selection affected traits, suggesting that genetic variation of plasticity within populations enabled individuals to rapidly evolve plasticity in response to high temperature. We found that short-term selection by high temperature increased plasticity for growth rate in all populations. Fecundity was higher in populations from fishless lakes and body size showed greater plasticity in populations from warm lakes (long-term selection). Neither body size nor fecundity were affected by short-term thermal selection. These results demonstrate that plasticity is an important component of the life-history response of *Daphnia*, and that genetic variation within populations enabled rapid evolution of plasticity in response to selection by temperature.

Keywords: adaptation, climate change, *Daphnia pulicaria*, introduced fish, life-history, phenotypic plasticity

Introduction

Rapid environmental change including changes in temperature can push species beyond their physiological boundaries, threatening their persistence (Parmesan 2006). When dispersal to suitable habitats is limited, populations can be rescued from extinction through two distinct but non-exclusive mechanisms: genetic adaptation, or phenotypic plasticity (Merilä and Hendry 2014). Genetic adaptation occurs by shifts in gene frequencies (Bell and Collins 2008), while phenotypic plasticity involves changes in traits without changes in DNA that can occur by mechanisms such as shifts in gene expression or DNA methylation (Lande 2009, Chevin et al. 2010). Understanding the relative importance of genetic adaptation and phenotypic plasticity as mechanisms

to cope with environmental change is crucial for predicting population persistence.

Recent studies demonstrate that genetic adaptation can rescue populations from extinction in response to changing climatic conditions (Nussey et al. 2005, Bradshaw 2006, Bradshaw and Holzapfel 2008), including rapid adaptation of increasing thermal tolerance (Geerts et al. 2015, Padfield et al. 2016). Adaptive responses can prevent population decline if there is sufficient genetic variation and selection on heritable traits that increases fitness (Gomulkiewicz and Holt 1995). However, there is no consensus as to how effective microevolution will be in mitigating consequences of ongoing environmental changes. In fact, if insufficient standing genetic variation is present in a population, or if migration is too slow to introduce new adaptive genotypes, a population may decline to extinction before evolutionary rescue can occur (Carlson et al. 2014). Hence, plasticity may play an important role as a mechanism to help populations to cope with rapid environmental change because plasticity can enable organisms to rapidly adjust to novel conditions (Charmantier et al. 2008, Gienapp et al. 2008, Merilä 2012, Munday et al. 2013).

Plasticity is expected to be favored and maintained by natural selection in variable environments. Theory predicts that plasticity will evolve in more heterogeneous environments with reliable cues, where its benefits outweigh its costs and genetic basis for plasticity exists in the population (Berrigan and Scheiner 2004, Chevin and Hoffman 2017). A powerful way to evaluate the relationship between environmental heterogeneity and plasticity is to compare populations arrayed along natural temperature gradients in latitude or elevation (Parmesan and Yohe 2003, Ghalambor et al. 2007, Deutsch et al. 2008, Hoffmann and Sgrò 2011). The degree of thermal plasticity has been shown to be proportional to the magnitude of temperature variation experienced in the local environment (Addo-Bediako et al. 2000, Khaliq et al. 2014). Thus, populations with different environmental histories may differ in the level of plasticity they present, which in turn may cause divergence in their response to novel selective pressures (Adams and Collyer 2009).

Temperature is one of many aspects of the environment undergoing rapid change (Sala et al. 2000) and selection imposed by other environmental changes could influence population vulnerability to thermal stress (Parmesan 2006). For instance, water fleas (genus *Daphnia*), a dominant freshwater zooplankter, respond similarly to predation by fish and high temperature because both exert pressure on the same traits and in the same direction, including smaller size and earlier age at maturity (Taylor and Gabriel 1993, Moore et al. 1997, De Meester et al. 2011). Previous studies have shown that elevation and fish predation can have important consequences for populations and communities. For instance, lake surveys in the Sierra Nevada (CA) showed that communities sympatric with fish at all elevations contain taxa characteristic of low elevation fishless lakes (Symons and Shurin 2016). Selection by fish predation and warmer temperatures tend to result in a decrease in body size, which reduces the ability of fish to detect *Daphnia*, and higher investment in reproduction (Riessen 1999). Therefore, both biotic and abiotic factors can drive population responses to warming (Tseng and O'Connor 2015).

Here we examine how biotic and abiotic selection interact to influence thermal plasticity in *Daphnia* populations originating from different long-term (lake conditions) and short-term (two-year mesocosms) environments. These *Daphnia* populations are native to alpine lakes in the Sierra Nevada (CA). The populations originate from lakes that vary in temperature due to elevation, and fish presence due to a century of salmonid stocking in these historically fishless lakes (hereafter long-term selection). We collected populations from high and mid-elevation lakes with and without fish predators, and then exposed them to cold and warm temperatures in a mesocosm experiment for two years (hereafter short-term selection). We then isolated clones from the field experiment and used a common-garden laboratory experiment to determine how selection on short- and long-time scales influenced the degree of phenotypic plasticity in *Daphnia* life-history in response to temperature.

We predicted that local adaptation would result in clones with the highest fitness in their home environment condition, i.e. 1) populations from cold lakes would exhibit higher fitness at low temperature, while populations from warm lakes would have higher fitness at higher temperature (crossing reaction norms). We also expected that 2) after two years of selection populations would evolve greater levels of plasticity in response to increased maximum temperature in the warm mesocosm treatment (i.e. steeper slopes of the reaction norms), since they would be experiencing higher temperatures.

Material and methods

Thermal field experiment

To determine how long- and short-term selection by temperature and fish predation influence life-history responses to temperature, we exposed populations of *Daphnia pulicaria* collected from four different categories of lakes (cold or warm, with fish present or absent), to high or low temperature (19°C and 13°C summer averages respectively) in field mesocosms that mimicked lake environments at two elevations (Symons 2017, Supplementary material Appendix 1 Table A1, Fig. A2). In July 2013, plankton and sediment were collected in 12 lakes located in Sierra Nevada (CA) (Supplementary material Appendix 1 Table A1). Lakes were categorized by elevation, high and low, and by presence or absence of fish, thus we had four lake categories: warm (low elevation) with fish, warm (low elevation) without fish, cold (high elevation) with fish, and cold (high elevation) without fish. Collections were made from three lakes within each category to inoculate the tanks in order to insure genetic and species diversity within each community type. Plankton were collected at the deepest point in the lake by drawing a 30 cm

diameter and 1 m length zooplankton net through the water column, starting 1 m above the lake bottom. Live plankton from the same lake category were mixed together to establish experimental communities. In addition, we collected 6 liters of sediment from the shore of each lake in order to include resting stages of invertebrates in the inoculum.

In order to initiate the thermal selection experiment we placed 1000-l mesocosms in UC Natural Reserves at two different elevations: 1200 m at the Sierra Nevada Research Station in Wawona and 3093 m at White Mountain Research Center. At each elevation we established five replicate mesocosms per lake category for 20 mesocosms in total at each elevation. We divided sediment equally among replicates of the same lake category and inoculated zooplankton at the mean density found in the lakes from the same category. We found that the community composition in the mesocosm experiment reflects general patterns found in natural lakes (Symons 2017). The complete design of the thermal field experiment is given in Symons (2017), and includes 20 additional mesocosms per elevation for treatment with fish predators (rainbow trout) present. No *D. pulicaria* persisted in mesocosms with fish, therefore the fish treatment was excluded from this study.

After two years, *D. pulicaria* adult females from each mesocosm were selected to establish maternal lineages. Two years of selection would correspond to about 30–50 generations during spring and summer in these populations based on what was found in the common-garden experiment. Maternal lines that survived came from 12 different warm mesocosms and seven different cold mesocosms (Supplementary material Appendix 1 Table A3). Mortality of maternal lines occurred during transportation from the field to the lab and acclimation to lab conditions. *Daphnia* produced ephippia (dormant eggs resulting from sexual reproduction) in the mesocosms, indicating that genetic diversity was present within and between mesocosms, but we did not establish whether maternal lines were genetically distinct. We quantified life-history parameters of maternal lines isolated from the mesocosms at two incubation temperatures: 13°C and 17°C ($\pm$1°C – hereafter referred to as 'test temperatures') under standardized laboratory conditions. Each maternal line was grown at the two test temperatures in the lab, and we constructed life tables for each one of the total 89 *D. pulicaria* maternal lines that survived. Our approach allowed us to partition the phenotypic response to selection by temperature over long (as determined by the lake of origin) and short, i.e. two years (as determined by the temperature in the mesocosm experiment) time scales.

Life-history experiment

This experiment consisted of 89 maternal lines total (replicates) obtained across all lake categories (four) and mesocosm temperatures (two). Each maternal line was grown at two test temperatures in the lab. To minimize maternal effects, each maternal line was cultured individually in a separate 50 ml tube filled with COMBO medium (Kilham et al. 1998)

under standardized conditions (17 ± 1°C and photoperiod 12:12 L:D) for two generations. All animals were fed live culture of the green alga *Nanochloropsis* sp. at a constant high rate of 24×10^6 cells per day. Neonates of the second clutch of the second generation were randomly assigned to each of the two test temperatures (13°C and 17°C). After culturing the animals for an additional two generations at their test temperature, juveniles from the second clutch were used as the experimental generation. Individuals were monitored daily and transferred every 48 h to clean jars with fresh media until they produced their third clutch. We scored the following life-history variables: age at maturity (when individual released eggs in the brood pouch), size at maturity, and age and number of offspring from each clutch. Data for the first three clutches were used to calculate intrinsic population growth rate (including only those individuals that survived for the duration of the experiment) for each maternal line following the Lotka–Euler equation (Roff 1997).

Statistical analysis

Correlations between life history traits were tested using Pearson's correlation tests (Supplementary material Appendix 1 Fig. A4). We analyzed the effects of the treatments using linear mixed-effects models for each trait using the lmer function from the lmerTest package in the statistical software R (Kuznetsova et al. 2017, <www.r-project.org>) implemented with restricted maximum likelihood estimation. We also used a cross-validation approach (the upSample function from the caret package and vfold_cv function from the rsample package; Kuhn and Wickham 2017, Kuhn 2018, <www.r-project.org>) to confirm that our results were not influenced by sample size differences (Supplementary material Appendix 1 Fig. A6). For each response variable, lake elevation, presence or absence of fish, mesocosm temperature and test temperature were modeled as fixed effects, and maternal line was nested within mesocosm as a random effect. We used the same procedure for number of offspring, but included age as an explanatory variable in the model as well. Any interaction that includes test temperature indicates an effect on the level of plasticity, i.e. effects on the slope of the reaction norms. We started with the most complex models for fixed effects (the random effect was kept in all models) and dropped higher order interactions if they did not significantly improve model fit (using log-ratio tests) until we arrived at a best-fit model. All variables, except intrinsic growth rate, were log transformed after visual inspection of data distribution.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1jj472j> (Cavalheri et al. 2018).

Results

The linear mixed-effects model revealed a range of factors that influenced life history (Table 1). All *Daphnia pulicaria*

Table 1. Results of stepwise model selection between long- and short-term selection and their interactions for *Daphnia pulicaria* life-history traits. Bold indicates significant p-values (< 0.05).

	Estimate	SE	df	T value	Pr(>|t|)
Age at maturity					
(Intercept)	2.335	0.027	175	85.099	**<0.001**
Lake temperature (L)	0.018	0.022	175	−0.843	0.400
Fish in the lake (F)	0.010	0.022	175	−0.462	0.644
Mesocosm temperature (M)	−0.015	0.022	175	−0.705	0.482
Test temperature (T)	−0.582	0.022	175	−26.153	**<0.001**
Size at maturity					
(Intercept)	0.339	0.020	32.50	16.932	**<0.001**
Lake temperature (L)	−0.038	0.022	15.87	−1.735	0.102
Fish in the lake (F)	0.011	0.021	21.24	0.520	0.608
Mesocosm temperature (M)	−0.013	0.021	24.32	−0.633	0.532
Test temperature (T)	0.054	0.021	14.67	2.491	**0.013**
L×F	−0.026	0.020	12.73	−1.288	0.220
L×M	0.037	0.020	12.38	1.833	0.091
L×T	0.050	0.019	14.75	2.531	**0.012**
F×M	0.060	0.020	11.15	0.293	0.774
F×T	−0.029	0.019	14.76	−1.499	0.136
M×T	0.047	0.020	14.73	0.002	0.998
Intrinsic growth rate					
(Intercept)	0.134	0.001	127	11.268	**<0.001**
Lake temperature (L)	−0.009	0.001	127	−0.791	0.430
Fish in the lake (F)	0.000	0.001	127	0.018	0.985
Mesocosm temperature (M)	0.000	0.001	127	−0.680	0.497
Test temperature (T)	0.116	0.001	127	9.678	**<0.001**
L×F	0.001	0.001	127	1.035	0.302
L×M	0.001	0.001	127	1.171	0.243
L×T	0.000	0.001	127	0.791	0.675
F×M	−0.002	0.001	127	−1.864	0.094
F×T	−0.001	0.001	127	−1.621	0.387
M×T	0.002	0.001	127	2.651	**0.004**

maternal lines showed life-history plasticity in response to test temperature. Age at maturity was only affected by test temperature (T, p<0.001) and decreased 4.5 ± 0.07 days on average when clones were grown at 17°C compared with clones tested at 13°C regardless of the previous conditions experienced by the maternal line (Fig. 1A–B).

Daphnia pulicaria were smaller at maturity at test temperature 13°C compared to 17°C by 0.1 ± 0.01 mm on average (Fig. 1C–D). However, the impact of test temperature on body size depended on lake elevation (L×T, p=0.012), indicating different slopes of the reaction norms between populations from warm and cold lakes. Maternal lines from warm lakes typically exhibited greater plasticity in size at maturity than those from cold lakes (Fig. 2, long-term selection), with crossing reaction norms where warm lake populations matured at smaller size at 13°C but larger size at 17°C.

The number of offspring produced per clutch was influenced independently by fish presence in the ancestral environment. Individuals from lakes with fish had 0.6 ± 0.16 fewer offspring on average than clones from fishless lakes (F, p=0.030, Table 2). Fecundity was also influenced by an interaction between age and test temperature (age×T, p=0.019, Table 2). As an individual ages, it produces more offspring per clutch, but the increase in number of offspring

per clutch is greater when individuals were tested at 17°C compared to 13°C (Fig. 3). The number of offspring produced at different test temperatures also varied with mesocosm temperature (M×T, p=0.004, Table 2). At 13°C maternal lines from cold mesocosms showed a steeper slope than those from warm mesocosms, while the opposite is seen for maternal lines tested at 17°C (Fig. 3).

Intrinsic growth rate was approximately two times greater at test temperature 17°C ($0.25\times$day^{-1}) than at test temperature 13°C ($0.12\times$day^{-1}; T, p<0.001). An interaction between mesocosm temperature and test temperature revealed that the intrinsic growth rate of maternal lines from warm mesocosms increased by $0.03\times$day^{-1} more than maternal lines from cold mesocosms when grown at 17°C compared to 13°C (M×T, p=0.004; Fig. 1E–F), i.e. populations that spent two years in warm mesocosms showed steeper slopes of the reaction norms than ones from cold mesocosms (Fig. 1E–F). All individuals reared in the 13°C test temperature had the same growth rate, regardless of long- or short-term selection while differences among lake and mesocosm treatments were expressed at 17°C. Specifically, at 17°C, *Daphnia* from warm mesocosms had a higher intrinsic growth rate compared to maternal lines from cold mesocosms (Fig. 2 short-term selection).
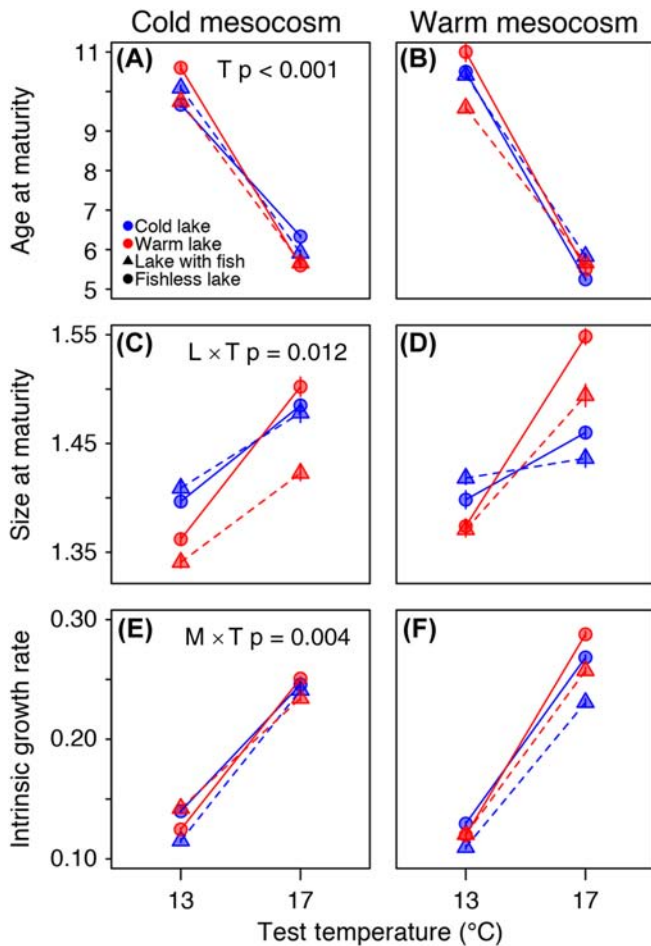
Figure 1. Means ± 1 SEM of age at maturity in days (A, B), size at maturity in millimeters (C, D) and intrinsic growth rate (E, F) of the populations of *Daphnia pulicaria* as a function of test temperature. Populations that spent two years in cold mesocosms (elevation: 3093 m) are shown on the left, and populations in warm mesocosms (elevation: 1200 m) are on the right. Significant effects for each trait after model selection are shown in the left panel (for letter reference Table 1). Red symbols indicate populations from warm, low elevation lakes (elevation: 2399–2801 m), and blue symbols are clones from cold lakes (elevation: 3150–3337 m). Circles indicate fishless lakes and triangles lakes with fish.

Discussion

We found evidence for the influence of both the short- and long-term selective environment on life-history traits and growth rates of *Daphnia pulicaria* populations from California mountain lakes. While the response of individual life-history traits to temperature showed the imprint of the ancestral lake environment, plasticity in population growth rate was most influenced by selection over the past two years. Together, these results suggest that rapid evolution of life-history plasticity maintains population growth near the optimum for *Daphnia*, although different life-history traits varied in their response to short-term selection. Such rapid

evolution of plasticity may have arisen from de novo mutations in the experimental populations or, perhaps more likely, selection among coexisting clones with variable responses to temperature within lakes found at the same elevation. Our results suggest that *Daphnia* populations display considerable adaptive potential to respond to changes in temperature within relatively short time scales.

Our data add to the growing body of evidence for evolutionary response to temperature-driven selection in *Daphnia* populations. In a study with *D. pulex*, Van Doorslaer et al. (2010) observed an effect of short-term selection treatments in size at maturity, as clones from heated mesocosms (24°C) reached maturity at a larger body size than those from non-heated mesocosms (20°C), indicating a microevolutionary response to temperature. Similarly, we found that *Daphnia* were larger on average at the warmer test temperature. This result contradicts the general expectation that warm temperature should result in decreases in size (Deutsch et al. 2008, Daufresne et al. 2009). Smaller size at high temperatures increases heat tolerance (Geerts et al. 2015, Brans et al. 2017) and enables more efficient oxygen transport. However, the larger size at higher temperature we observed could have arisen because 17°C is an intermediate temperature, hence, not warm enough to cause effects of thermal stress that produces smaller size.

In addition, the level of plasticity in size at maturity depended on the water temperature at the lake of origin as *Daphnia* populations from warm lakes had higher thermal plasticity than populations from cold lakes. However, size at maturity did not respond to short-term temperature selection, suggesting that this trait may evolve more slowly, or that less genetic variation for plasticity may be maintained within populations for size at maturity than for other life-history traits.

Populations that originated from warm lakes showed greater thermal plasticity in size at maturity than populations from cold lakes by being both larger at higher temperatures and smaller at colder temperatures, consistent with our hypothesis that populations are locally adapted to the thermal conditions in their environment. This result agrees with studies of other *Daphnia* populations. For example, Chopelet et al. (2008) found a similar pattern for metabolic rates in a comparison of subarctic and temperate populations of *D. magna* tested at 15°C and 25°C. Metabolic cold adaptation, a counter gradient variation that occurs when genetic differences counteract temperature effects (Krogh 1916) suggests that populations of ectotherms that inhabit colder environments should have increased metabolic rates to compensate for the negative effect of low temperatures on growth rates and, possibly, reaching a larger size. However, cold adapted organisms may not be able to maintain their metabolism at warm temperatures, at the same level as organisms from warm environments (Conover and Schultz 1995, Gaitán-Espitia and Nespolo 2014), thus metabolism in warm conditions would be lower, affecting body size. Our results support the cold metabolism hypothesis if large size
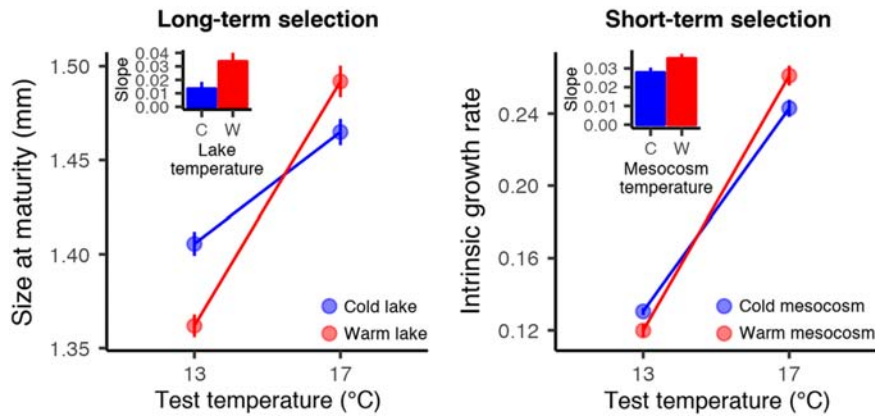
Figure 2. Effect of long- and short-term selection on level of plasticity in *Daphnia pulicaria* populations. Long-term selection: means ± 1 SEM of size at maturity across all populations from cold (blue) and warm (red) lakes in response to test temperature (13°C and 17°C). Inset shows the difference in slope for the reaction norms for size at maturity from populations of cold (C, blue, elevation: 3150–3337 m) and warm (W, red, elevation: 2399–2801 m) lakes. Short-term selection: means ± 1 SEM of intrinsic growth rate across populations from cold (blue, elevation: 3093 m) and warm (red, elevation: 1200 m) mesocosms in response to test temperature (13°C and 17°C). Inset shows the difference in slope for the reaction norms for intrinsic growth rate from populations of cold (C, blue) and warm (W, red) mesocosms.

at maturity confers fitness benefits, such as larger individuals producing larger clutches.

Changes in temperature might directly affect zooplankton physiology or indirectly influence zooplankton through bottom–up effects. Often the effects of temperature cannot be disentangled from the effects of nutrients, as low elevation, warm, lakes in Sierra Nevada (CA) also have greater primary productivity as well as higher levels of detritus and dissolved organic carbon (Symons and Shurin 2016). Hence, the effect of lake temperature on size at maturity could be confounded or be a synergistic response to high temperature and food availability, which can potentially increase growth and/or egg production of zooplankton (Kvile et al. 2016). In our common-garden experiment, food availability was controlled, leaving only the effect of temperature, thus indicating that differences in size at maturity are physiological adaptations in response to temperature.

We also found evidence of life-history evolution of *Daphnia* in response to the presence of fish in the ancestral environment, which was maintained over two years in mesocosms without fish. Long-term selection by fish did not show an interactive effect with test temperature, indicating that fish presence did not influence thermal plasticity. Populations from fishless lakes produced on average more offspring than populations sympatric with fish. Non-native fishes have been widely introduced into naturally fishless alpine lakes throughout the world with profound effects on native zooplankton species, including *Daphnia* (Knapp 1996). Previous work has documented contrasting life-history responses to fish predation where *Daphnia* populations from high predation environments show higher fecundity and faster development (Walsh and Post 2011, Stoks et al. 2016). Latta et al. (2007) compared life history of *D. melanica* among lakes throughout Sierra Nevada (CA) with different fish stocking histories and

Table 2. Results of stepwise model selection between age, long- and short-term selection and their interactions describing number of offspring in *Daphnia pulicaria*. Age and number of offspring were log-transformed. Bold indicates significant p-values (< 0.05).

| Number of offspring	Estimate	SE	df	T value	Pr(>|t|)
(Intercept)	0.173	0.304	653.392	0.569	0.569
Age	0.514	0.091	695.776	5.614	**<0.001**
Mesocosm temperature (M)	−0.171	0.258	502.705	−0.665	0.506
Test temperature (T)	0.025	0.230	699.070	0.112	0.910
Fish in the lake (F)	−0.561	0.258	460.858	−2.170	**0.030**
Lake temperature (L)	0.234	0.255	373.650	0.919	0.358
Age×M	0.012	0.074	693.231	0.162	0.871
Age×T	0.172	0.073	700.952	2.348	**0.019**
M×T	0.193	0.067	698.363	2.883	**0.004**
Age×F	0.133	0.074	691.552	1.797	0.072
M×F	−0.069	0.089	9.435	−0.779	0.455
T×F	0.081	0.067	699.438	1.206	0.228
Age×L	−0.109	0.073	688.015	−1.501	0.133
M×L	0.123	0.088	9.481	1.390	0.196
T×L	−0.022	0.066	698.031	−0.335	0.737
F×L	0.111	0.087	9.882	1.266	0.234
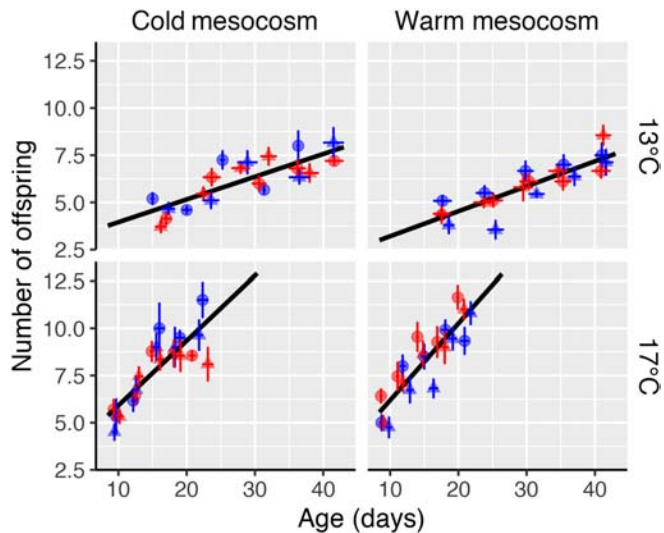
Figure 3. Average number of offspring against average age for each clutch measured for *Daphnia* reared at 17°C and 13°C test temperatures after spending two years in cold or warm mesocoms. Number of offspring ±1 SEM and age in days ±1 SEM are shown per population. Blue symbols represent populations from cold lakes and red, warm lakes. Triangles, populations from lakes with fish and circles, fishless lakes. Lines indicate relationship between age and number of offspring.

found that populations from lakes with fish showed reduction in number of eggs and size when compared to populations from fishless lakes. That study corroborates our findings that fishless populations had more offspring per clutch under all mesocosm and lab conditions, indicating that long-term selection by fish led to evolutionary divergence between fish and fishless populations. We did not have *Daphnia* populations from mesocosms with fish (i.e. short-term selection by fish) because *Daphnia* were extirpated from this treatment in the field experiment. It is possible that release from fish predation caused populations sympatric with fish to reduce resource allocation to reproduction, but further work will be necessary to isolate how evolutionary response to fish shape life-history responses to temperature.

We found that the intrinsic population growth rate of *Daphnia* populations was more closely associated with the selective environment of the past two years than the lake of origin, suggesting a rapid response of growth rates to selection by temperature. Indeed, clones isolated from the warm mesocosms in our experiment showed higher intrinsic growth rate at 17°C, and therefore steeper slopes of the reaction norms, than populations collected from the cold mesocosm, indicating increased levels of plasticity, which can also be seem by the steeper slope between age and number of offspring on clones from warm mesocosms tested at 17°C. This result supports our hypothesis, in that after two years of selection, populations would adjust plasticity to cope with shifting thermal environments (Lande 2009, Crispo et al. 2010). The ancestral environment had no lasting impact on

how population growth rate responded to temperature in our experiment. Similarly, Van Doorslaer et al. (2009) found that phenotypic plasticity increased the intrinsic growth rate for *D. magna* after only three months of thermal selection. By contrast, similar experiments with *D. magna*, *D. pulex* and *Simocephalus vetulus* revealed plastic growth rate responses to temperature, but no effect of short-term selection after six months of selection (Van Doorslaer et al. 2007, 2010), giving no indication of a microevolutionary response for population growth rate.

Our experiment showed that regardless of environmental history, all studied populations of *D. pulicaria* had elevated intrinsic growth rates at higher temperatures in response to short-term selection in warm mesocosms. Intrinsic growth rate is often greater at higher temperatures due to an increased metabolism (Mitchell and Lampert 2000, Weetman and Atkinson 2004), which permits rapid maturation and reduction in age at release of each clutch, resulting in larger populations in warmer temperatures in the absence of limiting conditions (Stich and Lampert 1981, Kingsolver and Huey 2008, Henning-Lucass et al. 2016). In fact, we found that number of offspring per clutch increased and the interval between clutches decreased in individuals that spent two years in warm mesocosms (Table 2, Fig. 3). Although populations in high elevation mesocosms probably underwent fewer generations in the time period of the experiment than populations in the low elevation treatment, populations at both elevations overwintered and produced ephippia (i.e. sexual reproduction occurred), which could have increased genetic variation, through recombination, increasing the scope for selection on plasticity.

Theory predicts that higher plasticity should evolve in more heterogeneous environments (Berrigan and Scheiner 2004). However, it is not always easy to identify the environmental factors that affect the development and maintenance of plastic responses. Analyses of temperature differences in our mesocosms experiment indicated higher temperature variation throughout the summer in cold mesocosms compared to warm mesocosms, but warm mesocosms had the greatest daily minimum and maximum temperatures (Supplementary material Appendix 1 Fig. A5). Studies with ectotherms show that temperature variation can have important impacts on life history traits (Tuck and Romanuk 2012, Hong and Shurin 2015). However, daily fluctuations in temperature can have qualitatively different effects at different mean temperatures (Vasseur et al. 2014, Kingsolver et al. 2015). Orcutt and Porter (1983) compared growth and reproductive responses of *D. parvula* in two fluctuating temperature regimes, high (15–25°C) and low (10–20°C) with those at the average and maximum constant temperatures at in each range (15°C and 25°C). They found that *Daphnia* at the constant maximum (25°C) and fluctuating high treatments (15–25°C) matured at the youngest age, and had the shortest time between clutches and the highest intrinsic growth rate, suggesting that fitness is higher at the warmest temperature. In addition, no differences were observed among *Daphnia* populations from

different latitudes in temperature performance curves as measured in life-table analyses (Mitchell and Lampert 2000), whereas a positive relationship was observed between thermal tolerance and the average temperature of the warmest month (Yampolsky et al. 2014). This supports our result of an increase in plasticity in the warmer mesocosm, suggesting that experiencing high temperatures continuously, instead of temperature variability, could be the cause of increasing plasticity.

We found variable life-history responses to temperature among *Daphnia* populations originating from lakes that differ in thermal and predation history and that had experienced two years of selection by different temperatures in the field. Our results indicate that *Daphnia* populations have high adaptive capacity to respond to environmental change in short time scales possibly through changes in the genetic composition of local populations. In addition, plasticity may evolve rapidly as maternal lines that had undergone two years of selection at warm temperatures showed greater thermal plasticity. This finding suggests that considerable adaptive potential within and among *Daphnia* populations arises from genetic and variation in phenotypic plasticity and may indicate that those populations could be resilient to temperature changes.

References

Adams, D. C. and Collyer, M. L. 2009. A general framework for the analysis of phenotypic trajectories in evolutionary studies. – Evolution 63: 1143–1154.

Addo-Bediako, A. et al. 2000. Thermal tolerance, climatic variability and latitude. – Proc. R. Soc. B 267: 739–745.

Bell, G. and Collins, S. 2008. Adaptation, extinction and global change. – Evol. Appl. 1: 3–16.

Berrigan, D. and Scheiner, S. M. 2004. Modeling the evolution of phenotypic plasticity. – In: DeWitt, T. J. and Scheiner, S. M. (eds), Phenotypic plasticity functional and conceptual approaches. – Oxford Univ. Press, pp. 82–97.

Bradshaw, A. 2006. Unravelling phenotypic plasticity – why should we bother? – New Phytol. 170: 639–641.

Bradshaw, W. E. and Holzapfel, C. M. 2008. Genetic response to rapid climate change: it's seasonal timing that matters. – Mol. Ecol. 17: 157–166.

Brans, K. I. et al. 2017. The heat is on: genetic adaptation to urbanization mediated by thermal tolerance and body size. – Global Change Biol. 23: 5218–5227.

Carlson, S. M. et al. 2014. Evolutionary rescue in a changing world. – Trends Ecol. Evol. 29: 521–530.

Cavalheri, H. B. et al. 2018. Data from: rapid evolution of thermal plasticity in mountain lake *Daphnia* populations. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.1jj472j>.

Charmantier, A. et al. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. – Science 320: 800–804.

Chevin, L. and Hoffman, A. A. 2017. Evolution of phenotypic plasticity in extreme environments. – Phil. Trans. R. Soc. B 372: 20160138.

Chevin, L. et al. 2010. Adaptation, plasticity and extinction in a changing environment: towards a predictive theory. – PLoS Biol. 8: e1000357.

Chopelet, J. et al. 2008. Plasticity of growth rate and metabolism in *Daphnia magna* populations from different thermal habitats. – J. Exp. Zool. A Ecol. Genet. Physiol. 309: 553–562.

Conover, D. and Schultz, E. T. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. – Trends Ecol. Evol. 10: 248–252.

Crispo, E. et al. 2010. The evolution of phenotypic plasticity in response to anthropogenic disturbance. – Evol. Ecol. Res. 12: 47–66.

Daufresne, M. et al. 2009. Global warming benefits the small in aquatic ecosystems. – Proc. Natl Acad. Sci. USA 106: 12788–12793.

De Meester, L. et al. 2011. Thermal genetic adaptation in the water flea *Daphnia* and its impact: an evolving metacommunity approach. – Integr. Comp. Biol. 51: 703–718.

Deutsch, C. A. et al. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. – Proc. Natl Acad. Sci. USA 105: 6668–6672.

Gaitán-Espitia, J. D. and Nespolo, R. F. 2014. Is there metabolic cold adaptation in terrestrial ectotherms? Exploring a latitudinal compensation using a common garden experiment of the invasive snail *Cornu aspersum*. – J. Exp. Biol. 217: 2261–2267.

Geerts, A. et al. 2015. Rapid evolution of thermal tolerance in the water flea *Daphnia*. – Nat. Clim. Change 5: 665–668.

Ghalambor, C. K. et al. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. – Funct. Ecol. 21: 394–407.

Gienapp, P. et al. 2008. Climate change and evolution: disentangling environmental and genetic responses. – Mol. Ecol. 17: 167–178.

Gomulkiewicz, R. and Holt, R. D. 1995. When does evolution by natural selection prevent extinction? – Evolution 49: 201–207.

Henning-Lucass, N. et al. 2016. Phenotypic plasticity in life-history traits of *Daphnia galeata* in response to temperature – a comparison across clonal lineages separated in time. – Ecol. Evol. 6: 881–891.

Hoffmann, A. A and Sgrò, C. M. 2011. Climate change and evolutionary adaptation. – Nature 470: 479–485.

Hong, B. C. and Shurin, J. B. 2015. Latitudinal variation in the response of tidepool copepods to mean and daily range in temperature. – Ecology 96: 2348–2359.

Khaliq, I. et al. 2014. Global variation in thermal tolerances and vulnerability of endotherms to climate change. – Proc. R. Soc. B 281: 20141097.

Kilham, S. S. et al. 1998. COMBO: a defined freshwater culture for algae and zooplankton. – Hydrobiologia 377: 147–159.

Kingsolver, J. G. and Huey, R. B. 2008. Size, temperature and fitness: three rules. – Evol. Ecol. 10: 251–268.

Kingsolver, J. G. et al. 2015. Fluctuating temperatures and ectotherm growth: distinguishing non-linear and time-dependent effects. – J. Exp. Biol. 218: 2218–2225.

Knapp, R. A. 1996. Non-native trout in natural lakes of the Sierra Nevada: an analysis of their distribution and impacts on native aquatic biota. – In: Sierra Nevada ecosystem project: final report to congress. Volume III: assessments, commissioned reports and background information. – Univ. of California, Centers for Water and Wildland Resources, Davis, pp. 363–407.

Krogh, A. 1916. The respiratory exchange of animals and man. – Longmans, Green and Co.

Kuhn, M. 2018. caret: classification and regression training. – R package ver. 6.0-80, <https://CRAN.R-project.org/package=caret>

Kuhn, M. and Wickham, H. 2017. rsample: general resampling infrastructure. – R package ver. 0.0.2, <https://CRAN.R-project.org/package=rsample>

Kuznetsova, A. et al. 2017. lmerTest package: tests in linear mixed effects models. – J. Stat. Softw. 82: 1–26.

Kvile, K. et al. 2016. Disentangling the mechanisms behind climate effects on zooplankton. – Proc. Natl Acad. Sci. USA 113: 1841–1846.

Lande, R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. – J. Evol. Biol. 22: 1435–1446.

Latta, L. C. et al. 2007. Rapid evolution in response to introduced predators II: the contribution of adaptive plasticity. – BMC Evol. Biol. 7: 1–9.

Merilä, J. 2012. Evolution in response to climate change: in pursuit of the missing evidence. – BioEssays 34: 811–818.

Merilä, J. and Hendry, A. P. 2014. Climate change, adaptation and phenotypic plasticity: the problem and the evidence. – Evol. Appl. 7: 1–14.

Mitchell, S. E. and Lampert, W. 2000. Temperature adaptation in a geographically widespread zooplankter, *Daphnia magna*. – J. Evol. Biol. 13: 371–382.

Moore, A. J. et al. 1997. Interacting phenotypes and the evolutionary process: I. direct and indirect genetic effects of social interations. – Evolution 51: 1352–1362.

Munday, P. L. et al. 2013. Predicting evolutionary responses to climate change in the sea. – Ecol. Lett. 16: 1488–1500.

Nussey, D. H. et al. 2005. Selection on heritable phenotypic plasticity in a wild bird population. – Science 310: 304–306.

Orcutt, J. D. and Porter, K. G. 1983. Diel vertical migration by zooplankton: constant and fluctuating temperature effects on life history parameters of *Daphnia*. – Limnol. Oceanogr. 28: 720–730.

Padfield, D. et al. 2016. Rapid evolution of metabolic traits explains thermal adaptation in phytoplankton. – Ecol. Lett. 19: 133–142.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – Annu. Rev. Ecol. Evol. Syst. 37: 637–669.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – Nature 421: 37–42.

Riessen, H. P. 1999. Predator-induced life history shifts in *Daphnia*: a synthesis of studies using meta-analysis. – Can. J. Fish. Aquat. Sci. 56: 2487–2494.

Roff, D. A. 1997. Evolutionary quantitative genetics. – Chapman & Hall.

Sala, O. E. et al. 2000. Global biodiversity scenarios for the year 2100. – Science 287: 1770–1774.

Stich, H. B. and Lampert, W. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. – Nature 293: 396–398.

Stoks, R. et al. 2016. Resurrecting complexity: the interplay of plasticity and rapid evolution in the multiple trait response to strong changes in predation pressure in the water flea *Daphnia magna*. – Ecol. Lett. 19: 180–190.

Symons, C. C. 2017. The ecology and evolution of top–down and bottom–up control in mountain lakes. – PhD thesis, Univ. of California San Diego, La Jolla, CA.

Symons, C. C. and Shurin, J. B. 2016. Climate constrains lake community and ecosystem responses to introduced predators. – Proc. R. Soc. B 283: 20160825.

Taylor, B. E. and Gabriel, W. 1993. Optimal adult growth of *Daphnia* in a seasonal environment. – Funct. Ecol. 7: 513–521.

Tseng, M. and O'Connor, M. I. 2015. Predators modify the evolutionary response of prey to temperature change. – Biol. Lett. 11: 20150798.

Tuck, C. and Romanuk, T. N. 2012. Robustness to thermal variability differs along a latitudinal gradient in zooplankton communities. – Global Change Biol. 18: 1597–1608.

Van Doorslaer, W. et al. 2007. Adaptive microevolutionary responses to simulated global warming in *Simocephalus vetulus*: a mesocosm study. – Global Change Biol. 13: 878–886.

Van Doorslaer, W. et al. 2009. Population dynamics determine genetic adaptation to temperature in *Daphnia*. – Evolution 63: 1867–1878.

Van Doorslaer, W. et al. 2010. Experimental thermal microevolution in community-embedded *Daphnia* populations. – Clim. Res. 43: 81–89.

Vasseur, D. A. et al. 2014. Increased temperature variation poses a greater risk to species than climate warming. – Proc. R. Soc. B 281: 20132612.

Walsh, M. R. and Post, D. M. 2011. Interpopulation variation in a fish predator drives evolutionary divergence in prey in lakes. – Proc. R. Soc. B 278: 2628–2637.

Weetman, D. and Atkinson, D. 2004. Evaluation of alternative hypotheses to explain temperature-induced life history shifts in *Daphnia*. – J. Plankton Res. 26: 107–116.

Yampolsky, L. Y. et al. 2014. Adaptive phenotypic plasticity and local adaptation for temperature tolerance in freshwater zooplankton. – Proc. R. Soc. B 281: 20132744.

Supplementary material (available online as Appendix oik-05945 at <www.oikosjournal.org/appendix/oik-05945>). Appendix 1.