Global Change Biology (2007) **13,** 878–886, doi: 10.1111/j.1365-2486.2007.01317.x

Adaptive microevolutionary responses to simulated global warming in *Simocephalus vetulus*: a mesocosm study

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Abstract

Although several studies suggest the occurrence of microevolutionary responses that may allow local persistence of populations under global warming, rigorous experimental proof is lacking. Here, we combined the realism and rigid, replicated experimental design of a large-scale mesocosm study where populations of the zooplankter *Simocephalus vetulus* were exposed for 1 year to different global warming scenarios with a life table experiment under laboratory conditions at three temperatures that eliminated confounding, nongenetic factors. Our results provide solid proof for a rapid microevolutionary response to global warming in both survival and the subcomponents of individual performance (age at reproduction and number of offspring), which may allow populations of *S. vetulus* to persist locally under predicted scenarios of global warming. Such microevolutionary responses may buffer changes in community structure under global warming and help explain the outcome of previous mesocosm studies finding only marginal effects of global warming at the community level.

Keywords: adaptive responses, experimental evolution, global warming, life history, life table experiment, mesocosm experiment, microevolution, rapid evolution, *Simocephalus*, temperature

Received 22 May 2006; revised version received 3 October 2006 and accepted 10 October 2006

Introduction

Temperature is a dominant factor structuring the distribution of taxa (Gaston, 2003). Global warming, therefore, poses a strong challenge to organisms. In response to global warming, many species are showing northward or elevational shifts in their distribution patterns (reviewed by Parmesan *et al*., 1999; Hill *et al*., 2002; Walther *et al*., 2002; Parmesan & Yohe, 2003; Wilson *et al*., 2005; Hickling *et al*., 2006) and concurrent microevolution of traits linked to these movements (Thomas *et al*., 2001; Hughes *et al*., 2003). These range shifts will ultimately affect the composition of local communities and biodiversity patterns (Sala *et al*., 2000). Alternatively, populations may persist locally through phenotypic plasticity and microevolution of life history traits to deal with increasing temperature (reviewed by Post *et al*., 2001; Pulido & Berthold, 2004; Jump & Penuelas, 2005), which may buffer against changes in community structure. Although many studies have provided indications for induced microevolution of life history traits associated with global warming, they are mainly of a longitudinal, correlational nature and did not manipulate temperature in a replicated design (e.g. Loe *et al*., 2005; Bradshaw & Holzapfel, 2006; Jonzen *et al*., 2006). These studies did not discriminate between genetic changes and maternal effects underlying the observed shifts in life history. As far as we know, there are no studies using experimental evolution experiments simulating global warming to rigorously evaluate the potential of populations to genetically adapt to global warming.

Aquatic ecosystems may be very vulnerable to temperature increases especially in combination with eutrophication (Jeppesen *et al*., 2003). Several studies have exposed freshwater communities to simulated global warming scenarios in outdoor mesocosms (e.g. McKee

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et al., 2002, 2003; Moss *et al*., 2003; Christoffersen *et al*., 2006), which mimic quite well the conditions in small, shallow lake ecosystems (Resetarits & Bernardo, 1998; Chalcraft *et al*., 2005). These studies have focused on the effects on community level end points and have typically not revealed important effects of global warming. McKee *et al*. (2002) concluded that the effects of increases in temperature caused by global warming on zooplankton communities of shallow lakes will most likely be subtle and, in the absence of other forcing variables (e.g. nutrient loading and fish predation), probably of insufficient magnitude to significantly alter ecosystem functional structures and processes during the next century. This result is surprising and needs to be verified under a broader range of conditions. Moreover, a mechanistic understanding of these observations is lacking. An absence of a strong response to climate change at the community level may be due to a predominance of generalist taxa that adapt to climate change with phenotypic plasticity. Alternatively, it may be the result of tracking of environmental changes through microevolutionary changes in the different species. In this latter scenario, adaptive evolution at the species level buffers shifts at the community level.

In the present study, our aim was to investigate the presence of a microevolutionary response to simulated global warming in *Simocephalus vetulus* (O. F. Müller 1776) under realistic conditions in large mesocosms. *S. vetulus* is a relatively large freshwater, cyclic parthenogenetic cladoceran that is an important competitor and grazer on algae in small lentic, often macrophyte rich habitats (Vakkilainen *et al*., 2004). *S. vetulus* has been reported to occur in most parts of Europe as well as in India, Africa and North America (Hann, 1995; J. Mergeay, personal communication; http://www.faunaeur.org). Given this species is widespread, it encounters a broad set of temperatures across its range. Zooplankton communities containing *S. vetulus* were inoculated in mesocosms and were exposed for 1 year to different temperature regimes. Their microevolutionary response to increased temperature was subsequently evaluated in a life table experiment at three temperatures. We scored key life history traits to obtain insight into the thermal dependency of survival, individual performance and its subcomponents. This methodology of experimental microevolution is a powerful and direct method to study the evolutionary potential and evolutionary dynamics of animals with a short generation time (Bennett, 2003), and it has been used successfully before in cladocerans to monitor the response to other selection pressures (e.g. Capaul & Ebert, 2003; Haag & Ebert, 2004). Our approach, therefore, combined the realism and rigid, replicated experimental design of a large-scale mesocosm study with a life table experiment under laboratory conditions at three temperatures that eliminated confounding, nongenetic factors.

Materials and methods

Mesocosm experiment

In August 2003, an outdoor mesocosm experiment was initiated involving exposure of zooplankton communities, harboring *Simocephalus* populations, to different combinations of nutrient loading (two levels: unenriched groundwater and weekly enriched groundwater with 54 mg P and 538 mg N per mesocosm) and temperature (three levels: ambient, A2 and A2+50%; see further). Each treatment combination was replicated four times, resulting in a total of 24 mesocosms. The 2800 L groundwater fed flow-through (retention time 74 days) mesocosms were placed in lowland Central Jutland, Denmark. They were inoculated with sediment containing resting eggs and a mixture of active plankton communities, including *S. vetulus*, from nearby lakes and ponds. Three-spined sticklebacks (*Gasterosteus aculeatus* Linnaeus 1758) were added to the mesocosms: one male was stocked in the low nutrient treatment and 12 males were added to the high nutrient treatment. Sediment and water were mixed from the different localities before being added in equal amount to all mesocosms. To further homogenize, water (including also *S. vetulus*) from the different tanks was thoroughly cross-mixed several times during the last 3 months before heating was initiated. For more details on the mesocosms, we refer to Liboriussen *et al*. (2005).

As the main goal of the present study was to investigate the microevolutionary response of *S. vetulus* to elevated temperature, we focused on the three temperature treatments at the lowest nutrient level (i.e. a subset of 12 mesocosms). Temperature treatments are based on the climate scenarios of the Intergovernmental Panel on Climate Change (IPCC) (Houghton *et al*., 2001). A first treatment consists of unheated control mesocosms, hereafter referred to as 'ambient.' The mesocosms of the second and third temperature treatments are heated according to the IPCC climate scenarios A2 and A2+50% downscaled to the regional level. Warming scenario 'A2' refers to the predicted temperature in the period 2071–2100, and is applied to the mesocosms as a heating scenario in which the temperature is constantly adjusted based on predictions of the monthly difference in temperature between 1961–1990 and 2071–2100 (Houghton *et al*., 2001). For instance, this scenario for Denmark predicts that the average changes in temperature in autumn and winter are more pronounced than in early summer. Scenario 'A2+50%' applies the change of 'A2' and adds another 50% to this change. In practice,

for the 'A2' scenario the temperature change applied ranged from 4.4 °C in September falling to 3.3 °C in December and reaching a minimum of 2.5 °C in June. For the 'A2+50%' scenario the figures were 6.6, 4.9 and 3.7 °C, respectively. Average temperatures in the sampling month August 2004 were 19.6, 23.4 and 25.4 °C in the three different temperature scenarios, respectively.

Life table experiment

To test for microevolution of *S. vetulus* in response to the mesocosm temperature treatments, we quantified key life history variables of clones from each mesocosm temperature treatment at three temperatures under laboratory conditions. In August 2004, we aselectively collected two clones of *S. vetulus* from each mesocosm. In this way, 24 clonal lines (2 individuals per mesocosm $\times$ 3 mesocosm temperature treatments $\times$ 4 replicate mesocosms) were established. At that moment, the animals had experienced for 1 year the temperature treatments in the outdoor mesocosms. We brought these clones to the laboratory in Belgium. To minimize maternal effects, the clones were cultured for more than two generations in separate 250 mL glass jars filled with dechlorinated tap water under standardized conditions (20 °C and photoperiod 14:10 L:D).

For the life table experiment, we scored life history variables in the first and second generation at three incubation temperatures: 18, 22 and 26 °C. Before the life table experiment, we transferred one juvenile from each clone to a 100 mL glass jar. All experimental animals were fed the green alga *Scenedesmus obliquus* at a constant high rate of 20×10^6 cells day^{-1} individual^{-1} to exclude any potentially confounding effects of food. When these juvenile females matured and produced their second clutch (still at 20 °C), one juvenile of this second clutch of each clone was randomly assigned to each of the three incubation temperatures. These individuals represented the first generation individuals of the life table experiment. They were checked daily and transferred to clean jars until they produced their second clutch. The second generation started off in a similar way with juveniles of the second clutch from mothers of the first generation. Both first and second generation animals were reared throughout the life table experiment at one of the three incubation temperatures. The only difference between the first and second generation animals is that the former were born from mothers reared at 20 °C.

In both generations, we scored the following life history variables: age at release of first and second clutch and number of offspring in first and second clutch. We calculated the population growth rate r iteratively following the Lotka–Euler equation: $\Sigma e^{-rx} \times l_x \times m_x = 1$ (Begon *et al.*, 2006), where l_x is the survivorship up to age x and m_x is the age-specific fecundity. Given that we calculate r only for surviving individuals, r here does not represent a value suitable for calculation of the real population growth rate, but is rather intended to quantify the performance of individuals. Hereafter, we will refer to r as 'performance.'

Statistics

A repeated measures analysis of variance (RM ANOVA) was performed in STATISTICA 6.0 (Statsoft Inc., Tulsa, OK, USA) to investigate the effect of mesocosm temperature and incubation temperature on clonal survival. As response variable we used the number of the two clones (0, 1 or 2) per mesocosm that survived until the second clutch of the second experimental generation. These values were (log + 1)-transformed to meet ANOVA assumptions. To avoid pseudoreplication, we considered the number of surviving clones from a given mesocosm at each incubation temperature as three repeats of that mesocosm. As the strongest test for a microevolutionary response to global warming would be a change in survival at the highest incubation temperature (26 °C), we also tested for a mesocosm temperature effect at this incubation temperature by setting an *a priori* contrast in the RM ANOVA.

Analyses on the other life history traits were done on the means of the two clonal lines obtained per mesocosm, thus using mesocosm as the experimental unit. To avoid pseudoreplication, we considered the mesocosm means of the response variables obtained at each incubation temperature as repeats of that mesocosm. The design, showing the relation between replicates (at the mesocosm temperature treatment level) and repeats (at the incubation temperature level) is illustrated in Fig. 1. On this figure, the enlarged mesocosm represents one replicate of the A2+50% mesocosm temperature treatment. Out of this single replicate two clones were isolated and kept as clonal lines in the laboratory at 20 °C. Afterwards, each clonal line was split up into three clonal sublines (one at each incubation temperature). The means of the two clonal sublines from the two different clonal lines at each incubation temperature were taken as the repeats of that mesocosm. The first repeat being the mean at 18 °C, the second repeat being the mean at 22 °C and the third repeat being the mean at 26 °C. All these analyses were run in PROC GLM of SAS v.9.1 (SAS Institute Inc., Cary, NC, USA). We tested for the effect of mesocosm temperature, incubation temperature and generation on performance in a two-level hierarchical RM ANOVA. We considered the three mesocosm means at each incubation temperature obtained during the first and second generation as repeats at a

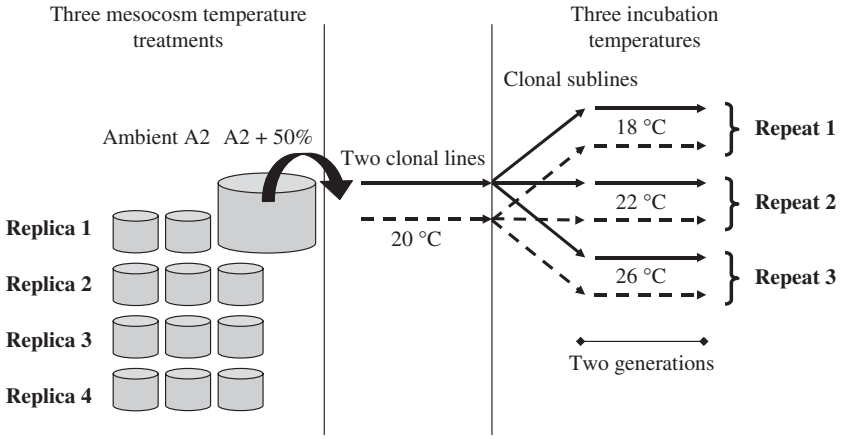

Fig. 1 Experimental design, emphasizing the relation between replicates (at the mesocosm temperature treatment level) and repeats (at the incubation temperature level).

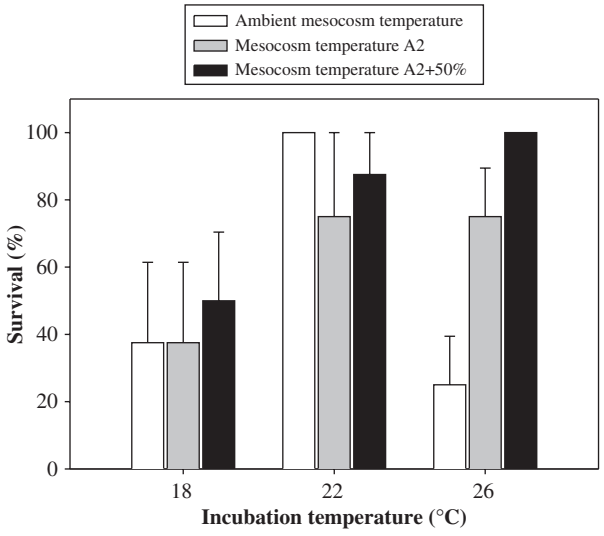

Fig. 2 Survival until the second clutch of the second generation of *Simocephalus vetulus* clones as a function of incubation temperature and mesocosm temperature. Means are given +1 standard error (SE). Note that for two treatment combinations survival was 100% so no SEs are given here. Plotted means were obtained by averaging the four mesocosm means for that combination of mesocosm temperature and incubation temperature. Each mesocosm mean was obtained by averaging the values of the two clonal lines per incubation temperature of that mesocosm (see Fig. 1).

higher level. We tested for effects of mesocosm temperature, incubation temperature and population on both subcomponents of our performance measure (age at release of first and second clutch and number of offspring in first and second clutch) in a three-level hierarchical RM ANOVA with as intermediate level repeats the mesocosm means at each incubation temperature of the first and second clutch. Response variables were not transformed as ANOVA assumptions were met. Only slight violation of the sphericity assumption of the RM ANOVA was present for incubation temperature, and here Huynh–Feldt adjusted *P*-values are given.

Results

Survival differed between the three incubation temperatures (RM ANOVA: $F_{2,18} = 5.95$, $P = 0.010$) with the highest overall survival (88%) at 22 °C and the lowest overall survival (42%) at 18 °C (Fig. 2). There was no significant effect of mesocosm temperature (RM ANOVA: $F_{2,9} = 1.02$, $P = 0.40$) or its interactions with incubation temperature (RM ANOVA: $F_{4,18} = 0.24$, $P = 0.11$). A contrast analysis focusing on the survival at the 26 °C incubation temperature did reveal a significant difference (contrast 'ambient' vs. 'A2+50%,' $F_{1,9} = 16.79$, $P = 0.0032$): at the highest incubation temperature (26 °C), survival of the clones obtained from the high mesocosm temperature treatment (A2+50%) was about four times higher compared with clones obtained from the ambient mesocosm temperature treatment.

Performance as measured by *r* increased with increasing incubation temperature (Table 1, Fig. 3). The significant incubation temperature × generation interaction revealed that overall at the two lowest incubation temperatures the performance of the individuals was higher in the second generation, while at the highest incubation temperature the inverse pattern occurred (Fig. 3). No significant effects of mesocosm temperature or interactions with mesocosm temperature were detected (Table 1).

Age at release of first and second clutch decreased with increasing incubation temperature (Table 2, Fig. 4). This was especially pronounced in first generation animals of mesocosm temperature treatment A2+50%.

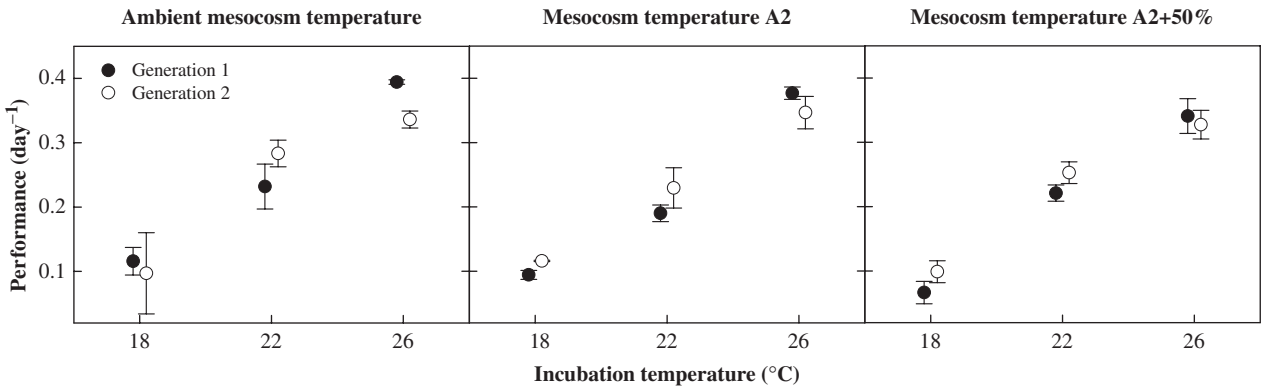

Fig. 3 Performance as measured by *r* of both generations of *Simocephalus vetulus* as a function of mesocosm temperature and incubation temperature. Means (see Fig. 2) are given ±1 SE.

Table 1 Repeated measures analysis of variance testing for the effect of mesocosm temperature and incubation temperature during two successive generations on performance as measured by *'r'*

	Performance		
Source of variation	df	*F*	*P**
Mesocosm temperature (MT)	2,4	0.87	0.49
Incubation temperature (IT)	2,8	85.23	<0.0001
Generation (G)	1,4	19.46	0.012
MT × IT	4,8	0.46	0.77
MT × G	2,4	2.19	0.23
IT × G	2,8	11.80	0.0041
MT × IT × G	4,8	1.47	0.30

The hierarchical repeated measures are incubation temperature (lower level) and generation (higher level).
*For incubation temperature and its interactions Huynh–Feldt adjusted *P*-values are given.

Table 2 Repeated measures analyses of variance testing for the effect of mesocosm temperature and incubation temperature during two successive generations on age at reproduction and number of offspring

	Age at reproduction			Number of offspring		
Source of variation	df	*F*	*P**	df	*F*	*P**
Mesocosm temperature (MT)	2,4	0.22	0.81	2,4	0.58	0.60
Incubation temperature (IT)	2,8	53.00	<0.0001	2,8	18.80	0.0019
Clutch (C)	1,4	372.57	<0.0001	1,4	26.92	0.0066
Generation (G)	1,4	3.76	0.12	1,4	6.53	0.063
MT × IT	4,8	0.71	0.61	4,8	0.95	0.48
MT × C	2,4	0.28	0.77	2,4	0.14	0.88
MT × G	2,4	4.54	0.093	2,4	38.46	0.0024
IT × C	2,8	23.44	0.00050	2,8	6.06	0.025
IT × G	2,8	3.28	0.092	2,8	1.04	0.40
C × G	1,4	1.55	0.28	1,4	5.87	0.073
MT × IT × C	4,8	1.83	0.22	4,8	0.94	0.49
MT × IT × G	4,8	6.85	0.011	4,8	2.72	0.11
MT × C × G	2,4	0.39	0.70	2,4	0.59	0.60
IT × C × G	2,8	0.00	1.00	2,8	1.33	0.32
MT × IT × C × G	4,8	0.87	0.52	4,8	1.94	0.20

The hierarchical repeated measures are incubation temperature (lowest level), clutch (intermediate level) and generation (highest level).
*For incubation temperature and its interactions Huynh–Feldt adjusted *P*-values are given.

At mesocosm temperature treatment A2, the pattern was somewhat less strong and more pronounced in second generation animals (mesocosm temperature × incubation temperature × generation). The decrease in age at reproduction with increasing incubation temperature was more pronounced in the second clutch (incubation temperature × clutch interaction) (Table 2, Fig. 4).

Overall, the number of offspring increased with increasing incubation temperature (Fig. 5). Both generations were differentially influenced by mesocosm temperature as indicated by the significant mesocosm temperature × generation interaction. While the overall pattern for the ambient mesocosm temperature treatment is that second generation animals produced more offspring than first generation animals, the opposite pattern occurred at mesocosm temperature treatment A2+50% (Table 2, Fig. 5). Second clutches were larger than first clutches, especially at the intermediate incubation temperature (22 °C) (incubation temperature × clutch) (Table 2, Fig. 5).

Discussion

Survival, performance and its subcomponents were highly dependent upon the rearing temperature in the incubators. Given the strong fitness links of these life history traits, temperature is a potential strong selection pressure in this species. Performance as measured by *r* of surviving animals was highest at 26 °C, suggesting that at this temperature population growth rate may potentially be high. However, only clones isolated from the heated mesocosms (A2+50% treatment) combined a high survival with a high performance in terms of development rate and clutch size. For clones obtained from the unheated control mesocosm temperature treatment (ambient), survival was highest at 22 °C and very low at 26 °C. Moreover, at the lowest and intermediate incubation temperatures, the performance of the animals increased going from the first to the second generation, while the opposite occurred at 26 °C. This suggests that for the clones living at the current temperature regime, 22 °C is the more optimal temperature and that living at 26 °C is stressful.

The about five times higher survival at 26 °C of clones exposed for 1 year to global warming scenario A2+50% compared with clones exposed to the unheated control temperature regime (ambient) strongly indicates rapid microevolution of the ability to cope with higher temperatures. To the best of our knowledge, this is the first rigorous experiment demonstrating microevolution of life history traits to simulated global warming that can exclude alternatives such as maternal effects. The poor survival of *S. vetulus* clones from the unheated control mesocosm treatment (ambient) at 26 °C, and this in contrast to the high survival of clones from the mesocosm treatment that simulated global warming scenario A2+50%, stresses the importance of this evolutionary shift to assure local population persistence under global warming. A likely physiological mechanism underlying

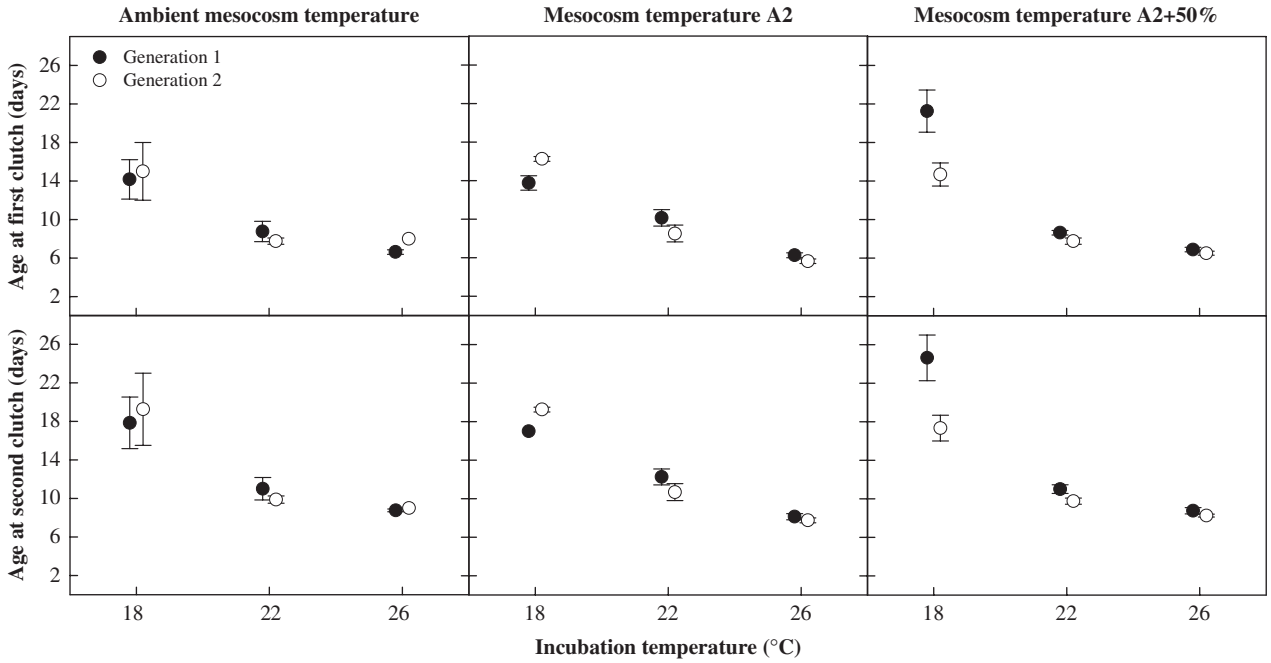

Fig. 4 Age at release of first and second clutch of *Simocephalus vetulus* as a function of mesocosm temperature, incubation temperature and generation. Means (see Fig. 2) are given ±1 SE.

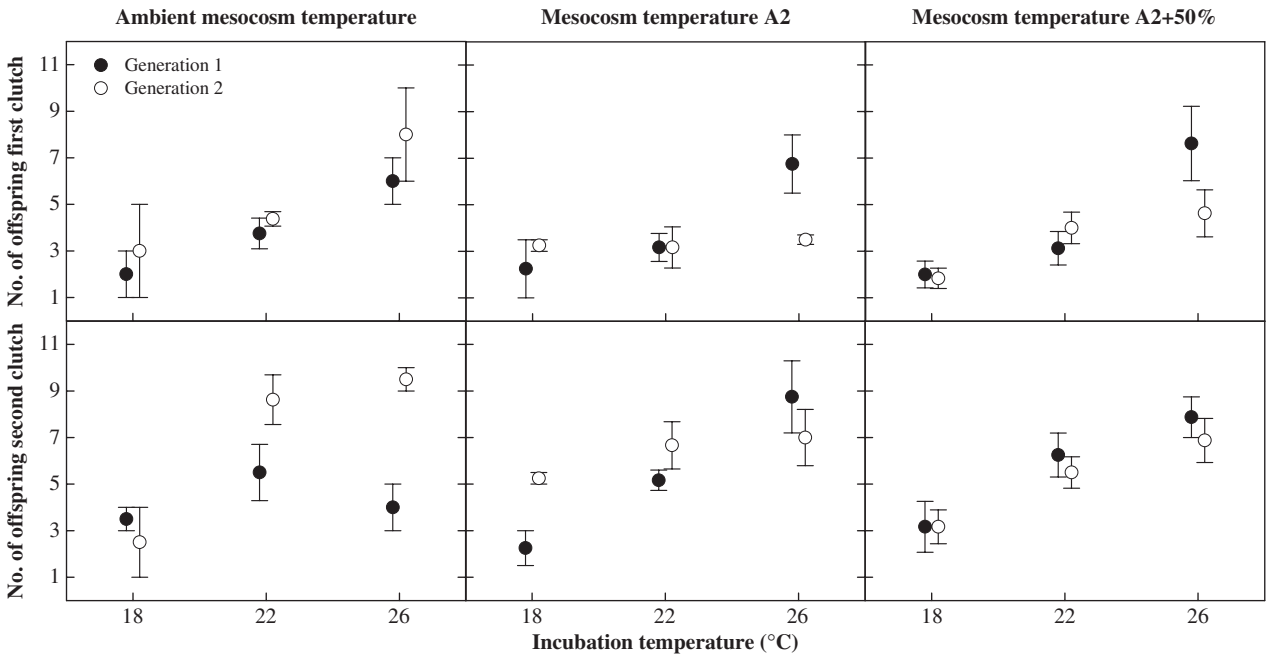

Fig. 5 Number of offspring in first and second clutch of *Simocephalus vetulus* as a function of mesocosm temperature, incubation temperature and generation. Means (see Fig. 2) are given ±1 SE.

this increased ability to cope with high temperatures is the upregulation of heat shock proteins (Riehle *et al*., 2003).

Clones obtained after 1 year of exposure to one of the three mesocosm temperature regimes did not differ in their performance, as measured by *r* of surviving animals. This indicates that no microevolution of this fitness measure occurred. However, the significant interactions of mesocosm temperature regime with incubation temperature and/or generation indicate microevolution in response to simulated global warming in both components of performance: age at reproduction and clutch size. Both subcomponents evolved differently in clones from the three mesocosm temperature regimes to generate the same patterns of performance (Figs 3–5). The general pattern of an increase in our performance measure with incubation temperature and the superimposed interactive effect with generation (an increase in performance in the second generation at 18 and 22 °C and a decrease at 26 °C) was attained in different ways depending on the selection history (mesocosm temperature treatment) of the clone. The contribution of both subcomponents to the pattern was not only dependent upon mesocosm temperature treatment but often also upon incubation temperature. The most important subcomponents to generate the pattern in performance were age at reproduction at the ambient mesocosm temperature regime (except at 22 °C) and mesocosm temperature regime A2+50% (except at 26 °C), and number of offspring at mesocosm temperature regime A2 (Figs 3–5). Analogous to our results, Mitchell & Lampert (2000) also reported no differences in juvenile growth rate, shown to be strongly correlated with the intrinsic rate of increase in *Daphnia* (Lampert & Trubetskova, 1996), among populations of *Daphnia magna* experiencing a differential thermal regime (i.e. positioned along a latitudinal gradient in Europe). However, these authors did not consider population differentiation in the subcomponents.

It is intriguing that animals evolved different strategies to reach the same value of our fitness measure (see also Angilletta *et al*., 2006; Pörtner *et al*., 2006). We have no explanation why different mesocosm temperature regimes lead to the evolution of the different strategies observed, except for the differences in survival, which are straightforward. Our setup cannot discriminate direct selective effects of temperature from indirect effects via changes in predation pressure, food availability or parasite prevalence. Whatever the cause of the evolution of these strategies, they may have fitness consequences that are not captured in our integrated measure of performance, which was obtained by rearing animals in the absence of competition by other clones, or other species, and without predators. For example, both age at reproduction and clutch size are life history traits that are important under fish predation pressure in zooplankton (e.g. Boersma *et al*., 1998; Spaak *et al*., 2000), and the nature of the strategy used by clones from the different mesocosm temperature regimes may reflect their success in the interaction with

the sticklebacks which were present in the mesocosms and had a strong effect on community components in the mesocosms (Meerhoff, 2006). As the species in the local community may determine the fitness of *S. vetulus*, and these effects may change with temperature depending upon the geographic origin of the accompanying species, different evolutionary outcomes to temperature increases may be possible depending upon the origin of the species in the local community. An additional complicating factor is that also this local community may change under global warming. However, in the present mesocosm experiment no pronounced differences in community structure linked to differential temperature regimes were observed (Meerhoff, 2006 and unpublished data).

In conclusion, we were able to demonstrate a rapid microevolutionary response (within 1 year) in survival, age at reproduction and offspring number to elevated temperatures in *S. vetulus* populations inoculated in large mesocosms. These responses may allow the species to maintain itself under the forecasted global warming scenarios, as evidenced by the persistence of *S. vetulus* populations in the mesocosms under all three climate scenarios (D. Verreydt, personal communication). Our data on survival suggest that without a microevolutionary response *S. vetulus* populations would probably not be able to maintain themselves under global warming. This indicates that the only marginal community response to global warming in previous mesocosm studies (e.g. McKee *et al*., 2002; Moss *et al*., 2003) may partly be related to compensating microevolutionary life history responses. This further illustrates the potential of rapid evolution to interfere with ecological processes (reviewed by Davis *et al*., 2005; Hairston *et al*., 2005). Our results on the response of age at reproduction and clutch size indicate that the patterns are not easy to predict, and are likely strongly structured by indirect effects of temperature on antagonistic interactions with competitors, predators and parasites. Experimental evolution approaches in mesocosms with simulated temperature regimes predicted under global change may be a powerful tool to evaluate the evolutionary potential of local populations to persist and may add strong complementary information to studies where current geographic gradients are used as proxies for *in situ* climate changes (e.g. Etterson & Shaw, 2001).

Acknowledgements

We thank Frank Landkildehus and Lone Liboriussen for running the mesocosms, Dino Verreydt for monitoring and providing information on the fate of *Simocephalus* in the different mesocosms. W. V. D. acknowledges a grant of the Institute for the Promotion of Innovation by Science and Technology in Flanders (IWT). R. S. is a postdoctoral fellow of the Fund for Scientific Research Flanders (FWO). This study was funded by the EU-IP project EUROLIMPACS GOCE-CT-2003-505540 and project OT/04/23 of the KULeuven Research Found. E. J. was also supported by the Danish Natural Science Research Council funded research project 'Consequences of weather and climate changes for marine and freshwater ecosystems. Conceptual and operational forecasting of the aquatic environment – CONWOY' (SWF: 2052-01-0034) and CLEAR (Villum Kahn Rasmussen Foundation).

References

Angilletta MJ, Bennett AF, Guderley H, Navas CA, Seebacher F, Wilson RS (2006) Coadaptation: a unifying principle in evolutionary thermal biology. *Physiological and Biochemical Zoology*, **79**, 282–294.

Begon M, Townsend CR, Harper JL (2006) *Ecology, from Individuals to Ecosystems*, 4th edn. Blackwell Publishing Ltd., Oxford.

Bennett AF (2003) Experimental evolution and the Krogh principle: generating biological novelty for functional and genetic analyses. *Physiological and Biochemical Zoology*, **76**, 1–11.

Boersma M, Spaak P, De Meester L (1998) Predator-mediated plasticity in morphology, life history, and behavior of *Daphnia*: the uncoupling of responses. *American Naturalist*, **52**, 237–248.

Bradshaw WE, Holzapfel CM (2006) Evolutionary response to rapid climate change. *Science*, **312**, 1477–1478.

Capaul M, Ebert D (2003) Parasite-mediated selection in experimental *Daphnia magna* populations. *Evolution*, **57**, 249–260.

Chalcraft DR, Binckley CA, Resetarits WJ Jr. (2005) Experimental venue and estimation of interaction strength: comment. *Ecology*, **86**, 1061–1067.

Christoffersen K, Andersen N, Søndergaard M, Liboriussen L, Jeppesen E (2006) Implications of climate-enforced temperature increases on freshwater pico- and nanoplankton populations studied in artificial ponds during 16 months. *Hydrobiologia*, **560**, 259–266.

Davis MB, Shaw RG, Etterson JR (2005) Evolutionary responses to changing climate. *Ecology*, **86**, 1704–1714.

Etterson JR, Shaw RG (2001) Constraint to adaptive evolution in response to global warming. *Science*, **294**, 151–154.

Gaston KJ (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, New York, NY, USA.

Haag CR, Ebert D (2004) Parasite-mediated selection in experimental metapopulations of *Daphnia magna*. *Proceedings of the Royal Society of London series B – Biological Sciences*, **271**, 2149–2155.

Hairston NG, Ellner SP, Geber MA, Yoshida T, Fox JA (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters*, **8**, 1114–1127.

Hann BJ (1995) Genetic variation in *Simocephalus* (Anomopoda, Daphniidae) in North-America – Patterns and consequences. *Hydrobiologia*, **307**, 9–14.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.

Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, Asher J, Huntley B (2002) Responses of butterflies to twentieth century

climate warming: implications for future ranges. *Proceedings of the Royal Society of London series B-Biological Sciences*, **269**, 2163–2171.

Houghton JT, Ding Y, Griggs DJ *et al*. (2001) *Climate Change 2001: The Scientific Basis*. Cambridge University Press, Cambridge, UK.

Hughes CL, Hill JK, Dytham C (2003) Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries. *Proceedings of the Royal Society of London series B-Biological Sciences*, **270**, S147–S150.

Jeppesen E, Søndergaard M, Jensen JP (2003) Climate warming and regime shifts in lake food webs–some comments. *Limnology and Oceanography*, **48**, 1346–1349.

Jonzen N, Linden A, Ergon T *et al*. (2006) Rapid advance of spring arrival dates in long-distance migratory birds. *Science*, **312**, 1959–1961.

Jump AS, Penuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, **8**, 1010–1020.

Lampert W, Trubetskova I (1996) Juvenile growth rate as a measure of fitness in *Daphnia*. *Functional Ecology*, **10**, 631–635.

Liboriussen L, Landkildehus F, Meerhoff M *et al*. (2005) Global warming: design of a flow-through shallow lake mesocosm climate experiment. *Limnology and Oceanography Methods*, **3**, 1–9.

Loe LE, Bonenfant C, Mysterud A *et al*. (2005) Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. *Journal of Animal Ecology*, **74**, 579–588.

McKee D, Atkinson D, Collings S *et al*. (2002) Macro-zooplankter responses to simulated climate warming in experimental freshwater microcosms. *Freshwater Biology*, **47**, 1557–1570.

McKee D, Atkinson D, Collings SE *et al*. (2003) Response of freshwater microcosm communities to nutrients, fish, and elevated temperature during winter and summer. *Limnology and Oceanography*, **48**, 707–722.

Meerhoff M (2006) *The structuring role of macrophytes on trophic dynamic in shallow lakes under a climate-warming scenario*. PhD thesis, National Environmental Research Institute, Silkeborg, Denmark, 156 pp.

Mitchell SE, Lampert W (2000) Temperature adaptation in a geographically widespread zooplankter, *Daphnia magna*. *Journal of Evolutionary Biology*, **13**, 371–382.

Moss B, McKee D, Atkinson D *et al*. (2003) How important is climate? Effects of warming, nutrient addition and fish on phytoplankton in shallow lake microcosms. *Journal of Applied Ecology*, **40**, 782–792.

Parmesan C, Ryrholm N, Stefanescu C *et al*. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

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

Pörtner HO, Bennett AF, Bozinovic F *et al*. (2006) Trade-offs in thermal adaptation: the need for a molecular to ecological integration. *Physiological and Biochemical Zoology*, **79**, 295–313.

Post E, Forchhammer MC, Stenseth NC, Callaghan TV (2001) The timing of life-history events in a changing climate. *Proceedings of the Royal Society of London series B – Biological Sciences*, **268**, 15–23.

Pulido F, Berthold P (2004) Microevolutionary response to climatic change. *Advances in Ecological Research*, **35**, 151–183.

Resetarits WJ Jr., Bernardo J. (1998) *Experimental Ecology: Issues and Perspectives*. Oxford University Press, New York, NY, USA.

Riehle MM, Bennett AF, Lenski RE, Long AD (2003) Evolutionary changes in heat-inducible gene expression in lines of *Escherichia coli* adapted to high temperature. *Physiological Genomics*, **14**, 47–58.

Sala OE, Chapin FS, Armesto JJ (2000) Biodiversity – global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Spaak P, Vanoverbeke J, Boersma M (2000) Predator-induced life-history changes and the coexistence of five taxa in a *Daphnia* species complex. *Oikos*, **89**, 164–174.

Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, Conradt L (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577–581.

Vakkilainen K, Kairesalo T, Hietala J *et al*. (2004) Response of zooplankton to nutrient enrichment and fish in shallow lakes: a pan-European mesocosm experiment. *Freshwater Biology*, **49**, 1619–1632.

Walther GR, Post E, Convey P *et al*. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wilson RJ, Gutierrez D, Gutierrez J, Martinez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, **8**, 1138–1146.