

# Local genetic adaptation generates latitude-specific effects of warming on predator–prey interactions

MARJAN DE BLOCK\*, KEVIN PAUWELS\*, MAARTEN VAN DEN BROECK\*, LUC DE MEESTER\* and ROBBY STOKS\*

\*Laboratory of Aquatic Ecology, Evolution and Conservation, University of Leuven, Debériotstraat 32, Leuven B-3000, Belgium

## Abstract

Temperature effects on predator–prey interactions are fundamental to better understand the effects of global warming. Previous studies never considered local adaptation of both predators and prey at different latitudes, and ignored the novel population combinations of the same predator–prey species system that may arise because of northward dispersal. We set up a common garden warming experiment to study predator–prey interactions between *Ischnura elegans* damselfly predators and *Daphnia magna* zooplankton prey from three source latitudes spanning >1500 km. Damselfly foraging rates showed thermal plasticity and strong latitudinal differences consistent with adaptation to local time constraints. Relative survival was higher at 24 °C than at 20 °C in southern *Daphnia* and higher at 20 °C than at 24 °C, in northern *Daphnia* indicating local thermal adaptation of the *Daphnia* prey. Yet, this thermal advantage disappeared when they were confronted with the damselfly predators of the same latitude, reflecting also a signal of local thermal adaptation in the damselfly predators. Our results further suggest the invasion success of northward moving predators as well as prey to be latitude-specific. We advocate the novel common garden experimental approach using predators and prey obtained from natural temperature gradients spanning the predicted temperature increase in the northern populations as a powerful approach to gain mechanistic insights into how community modules will be affected by global warming. It can be used as a space-for-time substitution to inform how predator–prey interaction may gradually evolve to long-term warming.

**Keywords:** common garden experiment, *Daphnia magna*, global warming, *Ischnura elegans*, latitude, predator–prey interactions, space-for-time substitution, thermal plasticity, thermal adaptation

Received 3 August 2012; revised version received 12 October 2012 and accepted 2 November 2012

## Introduction

One of the biggest challenges in ecology is to understand and predict the impact of global warming on species (Hughes, 2000; Gilman *et al.*, 2010; Zarnetske *et al.*, 2012). This has led many studies to document effects of temperature increases on individual species (Root *et al.*, 2003; Parmesan, 2006). Yet, species are embedded in communities and to arrive at more realistic predictions of species' responses and eventually community responses to global warming we need to take effects on species interactions into account (Araujo & Luoto, 2007; Berg *et al.*, 2010; Gilman *et al.*, 2010; Urban *et al.*, 2012b; Wernberg *et al.*, 2012). Interactions between trophic levels such as predator–prey interactions are thought to be particularly important in this context (Zarnetske *et al.*, 2012). Freshwaters are especially vulnerable to global warming (Woodward *et al.*, 2010), and strongly shaped by predator–prey interactions (Wellborn *et al.*, 1996). Temperature effects on predator–prey interactions may therefore increase our

mechanistic understanding of how global warming may change aquatic food webs (Kratina *et al.*, 2012), yet are surprisingly understudied in aquatic ecosystems (Abrahams *et al.*, 2007).

The majority of studies of warming effects on predator–prey interactions considered closed systems where no dispersal occurs (Gilman *et al.*, 2010). These revealed that warming may differentially affect organisms at different trophic levels and therefore affect the outcome of predator–prey interactions (Traill *et al.*, 2010). Most of these studies were, however, confined to a single latitude making it difficult to generalize across the species range. The few studies on latitudinal patterns in predator–prey interactions under common garden conditions showed predation rates to differ when conspecific predators from different latitudes feed on prey from a single latitude (Sanford *et al.*, 2003; Stoks *et al.*, 2012), and the vulnerability to predation to differ across latitudes for conspecific prey confronted with predators from a single latitude (Laurila *et al.*, 2008). Although such studies are very valuable in demonstrating that predator–prey interactions can show latitudinal patterns, they ignore potential effects of local adaptation of both predator and prey populations (Barton, 2011). A next

Correspondence: Robby Stoks, tel. +32 16323710, fax +32 16324575, e-mail: robbystoks@bio.kuleuven.be

step toward realism will be to set up experiments where the outcome of predator–prey interactions between combinations of both local predators and local prey is studied at different latitudes and at different temperatures.

We know much less of how species interactions change in response to global warming in open systems where organisms can track the changing climate by dispersal (Gilman *et al.*, 2010). Northward movements have been observed in many species (Parmesan *et al.*, 1999; Hickling *et al.*, 2006; Hassall & Thompson, 2010), leading to novel predator–prey interactions. The few studies that looked at this considered new sets of interacting predator and prey species (reviewed in Gilman *et al.*, 2010; Urban *et al.*, 2012a; but see Barton, 2011 for a study on nonconsumptive predator effects). Yet, intraspecific range movements are likely also widespread (Urban *et al.*, 2012a) and generate novel interactions in the sense that new combinations of predator and prey populations of the same species pair will interact.

Here, we study the thermal dependence of predator–prey interactions between an aquatic invertebrate predator and its zooplankton prey using predator and prey populations from three latitudes spanning >1500 km in Europe. To start exploring the consequences of global warming in open systems where dispersal can occur, we tested predators from each latitude at two temperatures with a mixture of prey from all three latitudes and quantified predator foraging rates and the relative vulnerabilities of prey. Such common garden experiments where predators from different latitudes are confronted with prey from different latitudes may also serve as an indirect space-for-time substitution (*sensu* Fukami & Wardle, 2005). As such they may inform how predator–prey interactions may gradually evolve when both predators and prey are subjected to long-term differences in temperature, thereby avoiding the extrapolation problem when strictly using short-term ‘shock’ experiments at one latitude to test future warming scenarios (Dunne *et al.*, 2004; Fukami & Wardle, 2005; Barton, 2011). As a model system, we looked at the interactions between *Ischnura elegans* damselfly larvae and *Daphnia magna* water fleas, a well-studied predator–prey combination (e.g., Thompson, 1978). Damselfly larvae are important intermediate predators in aquatic food webs (Johnson, 1991), and sensitive to climate change (Hassall & Thompson, 2008). *Daphnia* occupies a central position in aquatic food webs generating a large grazing pressure on the primary producers, and themselves being preferred food for both invertebrate and vertebrate predators (Miner *et al.*, 2012).

## Materials and methods

To test for the effects of temperature and source latitude of damselfly predators and *Daphnia* prey on the outcome of the predator–prey interactions we ran a series of predation trials with laboratory-reared predators and prey from three latitudes (southern, central, and northern Europe). Experimental temperatures were set at 20 and 24 °C, reflecting the mean water temperatures in shallow water bodies during summer in southern Scandinavia and southern France, respectively (see Data S1). The 4 °C temperature difference corresponds with the predicted temperature increase by 2100 under IPCC scenario A1FI (IPCC, 2007). This set up therefore is suitable for a space-for-time substitution. Throughout the rearing and predation trials animals were always kept at the same temperature. In the predation trials, only predators and prey reared at the same temperature were tested together as this is the most relevant combination in nature, also under global warming. Note that because *Daphnia* were reared for several generations in the laboratory and *Ischnura* damselflies from the egg stage (see below) any latitudinal patterns that we observe likely reflect genetic patterns of local adaptation. Although maternal effects may still play a role in shaping the foraging patterns for the damselfly larvae, previous study on the same species showed maternal effects to be nonsignificant for the associated life history trait growth rate and latitudinal differentiation in growth rates to be caused by selection (Shama *et al.*, 2011).

### Damselfly predators

As predator we used larvae of the damselfly *Ischnura elegans*, a very abundant damselfly in ponds occurring from mid-Spain to mid-Sweden (Gosden *et al.*, 2011). The larvae used for this experiment were a random subset of larvae from a large rearing experiment. During the summer of 2010, mated females were collected in the field at two shallow water bodies with fish at each of three latitudes: (1) southern latitude (southern France: Arandon 45°42'N, 5°25'E and Courtenay 45°43'N, 5°22'E), (2) central latitude (Belgium: Genk 50°57'N, 5°27'E and Leuven 50°51'N, 4°41'E), and (3) northern latitude (southern Sweden: Kalmar Dämme 56°40'N, 16°17'E and Långviken 56°39'N, 16°20'E). Females were allowed to oviposit *in situ* in wet filter paper. Per population, 10 egg clutches were transported to the laboratory in Belgium. Per egg clutch, the eggs were divided among water baths at 20 °C and at 24 °C. To minimize carry-over effects of the maternal environment, damselfly larvae were reared from the egg at one of the two test temperatures. Throughout the rest of the experiment, animals were kept at the assigned rearing temperature and a constant photoperiod (16:8 light:dark).

When eggs hatched, 150 larvae per combination of population and temperature (total of 900 larvae per temperature) were placed individually in 180 mL cups filled with aged tap water. Cups were placed in one of the three water baths per temperature. Larvae were fed *ad libitum* with *Artemia* nauplii. When larvae started molting into the final larval stage, cups were checked every second day for molted larvae and larvae

were used in the predation experiment (see below) when they were 5–6 days in the final instar. To homogenize hunger levels, all larvae were starved for 24 h prior to the predation trials.

### *Daphnia* prey

As prey we used the water flea *Daphnia magna*, a common zooplankton in ponds from southern Spain to mid-Scandinavia (De Gelas & De Meester, 2005), across its range, co-occurs with *I. elegans* predators. We tested two *D. magna* populations from two shallow water bodies with fish at each of three latitudes: (1) southern latitude (southern France: La Camargue 'Emp-runt des Cerisières Nord' 43°29'N, 4°40'E and 'Cerisières des Faïsses' 43°29'N, 4°41'E), (2) central latitude (Belgium: Leuven 50°51'N, 4°43'E and Oud-Heverlee 50°50'N, 4°39'E), and (3) northern latitude (Denmark: Brødstrup 55°58'N, 9°35'E and southern Sweden: Vomb 55°40'N, 13°32'E). We did not test *Ischnura* predators and *Daphnia* prey from the same pond as we were interested in local adaptation at the latitudinal level rather than at the pond level, yet at each of these ponds both species co-occurred. Dormant eggs were collected from the sediment. Eggs were hatched in a temperature room at 20 °C and a constant photoperiod (16:8 light:dark) and clones were kept as clonal lineages for several generations. Six clones per population were reared in 210 mL glass vials with aged tap water, fed daily  $1\text{--}2 \times 10^5$  cells *Scenedesmus obliquus* mL<sup>-1</sup>.

To establish experimental populations, for each clone, four sets of five juveniles were transferred to separate 500 mL glass vials. Two vials per clone were placed in a temperature room at 20 °C, the other two vials per clone were placed in a temperature room at 24 °C. To minimize maternal effects, clones were kept for two generations at these temperatures before their offspring (second to seventh clutch) was used in the predation experiment. Predation trials were run with subadult *Daphnia*. To test *Daphnia* at a similar physiological age, 3- to 4-day-old animals were used at 24 °C, and 4- to 5-day-old animals at 20 °C (based on Rinke & Vijverberg, 2005).

### Predation experiment

We set up a full factorial 2 (temperature)  $\times$  3 (damselfly source latitude)  $\times$  2 (damselfly populations per source latitude) experiment, where in each trial we exposed *Daphnia* prey from all three latitudes. This is a particularly strong design to directly compare the relative vulnerability of the *Daphnia* from different latitudes as they are all confronted with the same set of predator individuals in each predation trial. Depending on the simultaneous availability of damselfly larvae and *Daphnia* of the right age, each of the 12 treatment combination was replicated 7–11 times, resulting in a total of 114 predation trials. Each clone was used one or two times per temperature. When a clone was used twice per temperature, this was always with different individuals, and always in a unique combination with clones from the other two latitudes. Each damselfly larva was used in only one predation trial.

Predation trials were run in green 11 L buckets filled with 6 L aged tap water that was preheated to one of the two

rearing temperatures. Buckets were lighted from above with fluorescent bulbs. The circular shape of the ground surface prevented any clustering of *Daphnia* in the corners. To avoid any potential effects of room conditions (e.g. light intensity) all buckets of the predation trials of both temperatures were positioned in a random order at the same shelf in a temperature room at 24 °C. Water temperature in the buckets (also those of the 20 °C treatment) remained constant throughout the short predation trials.

At the start of a predation trial, we added 20 *Daphnia* individuals of a single clone from each of the three latitudes to a bucket (total of 60 *Daphnia*). *Daphnia* were allowed to acclimate for 60 min. Next, two damselfly larvae of the same population were gently released at the bottom of the bucket. This reflects natural densities of both *Ischnura* damselfly larvae (McPeck, 1998) and *Daphnia* prey (Young, 1979). Predation trials always started at noon and ran between 2 and 4 h (mean duration = 2.5 h, SE = 0.04 h, adjusted based on visual inspection of the buckets to avoid too low and too high numbers eaten). The mean number of *Daphnia* killed per trial was 24.0 (SE = 0.6, range: 10–39). Depending on the availability of predator and prey individuals of the right developmental stage several trials were run simultaneously. At the end of each trial, surviving *Daphnia* were collected, counted, and immediately frozen at –80 °C for later allozyme analyses to determine the proportion of survived *Daphnia* from each latitude (see Data S2). Nearly all (98.8%) *Daphnia* that were killed were consumed. To correct for potential mass differences among the damselfly predators of different populations, wet masses were taken to the nearest 0.01 mg just before the predation trials. For each clone by temperature combination at least three individual *Daphnia* were measured using a stereomicroscope to correct for potential size differences among clones. Background information on the age and mass of the damselflies and the size of the *Daphnia* used in the predation trials are presented in Data S3 and Data S4, respectively. Due to accidental thawing of some samples, we could only genotype the samples of 85 of the 114 predation trials. For final sample sizes per treatment combination see Fig. 2.

For each trial, we calculated two fully independent response variables: (1) damselfly foraging rate was expressed as the numbers of *Daphnia* eaten per hour, and (2) relative survival of *Daphnia* prey was calculated per trial as the number of *Daphnia* surviving per source latitude divided by the total number of surviving *Daphnia*.

### Statistical analyses

Analyses were run in PROC MIXED in SAS 9.2. In all analyses, damselfly population nested in latitude and each of the three *Daphnia* populations nested in latitude were included as random factors, but these were never significant indicating consistent response patterns between populations within a given latitude. First, we tested for effects of temperature and damselfly source latitude on damselfly foraging rates in an analysis of covariance (ANCOVA) with the mean *Daphnia* size and the number of surviving *Daphnia* per trial as covariates.

Second, we tested for effects of temperature and damselfly latitude on the relative survival of *Daphnia* prey in a repeated-measures ANCOVA (RM-ANCOVA) with the proportions of *Daphnia* survived from the southern and northern latitudes as repeats of the same predation trial (bucket) and with the mean *Daphnia* size per predation trial as a covariate. Initially, we also included the body mass of the damselfly predators and the number of surviving *Daphnia* per trial as covariates, but these were not significant (both  $P > 0.16$ ). Note, that we did not include the proportion of *Daphnia* from all three latitudes as repeats as these necessarily sum to 1. Proportions were arcsin (sqrt)-transformed. More specific hypotheses were tested using contrast analyses.

To test a priori expectations on local thermal adaptation (both of prey and predator) we set a first series of contrasts. Specifically, to test for local thermal adaptation in the southern *Daphnia* we tested whether their relative survival was higher at 24 °C (the temperature reflecting their latitude) than at 20 °C (the temperature reflecting the northern latitude). As local thermal adaptation of the damselfly predators may offset this thermal adaptation pattern in the prey, we tested this contrast separately for non-local (central and northern) predators and local (southern) predators. Similarly, as we expected that northern *Daphnia* would have a higher relative survival at 20 °C compared to 24 °C except with northern damselfly larvae, we set two analogous contrasts: a first contrast testing the temperature effect for the combined set of southern and central damselfly larvae and a second contrast testing the temperature effect only for northern damselfly larvae. Note that because neither of the experimental temperatures reflect the mean summer temperature at the central latitude, no specific contrasts with regard to local thermal adaptation were set for the central *Daphnia*.

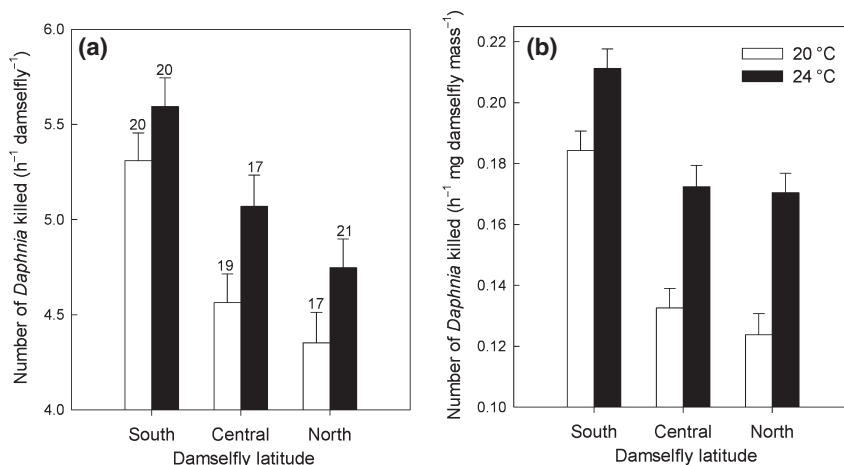
A second series of contrasts explored the outcome of novel predator–prey interactions due to northward movements of prey and/or predators. Given that we combined *Daphnia* from all three latitudes in each predation trial the most

straightforward scenario to test is the one where *Daphnia* from lower latitudes move northward under global warming and meet northern *Daphnia* and damselfly predators. The associated contrast (1) compared the relative survival of central and southern *Daphnia* vs. northern *Daphnia* in the presence of northern predators at 24 °C. A related contrast (2) compared the relative survival of southern vs. central *Daphnia* in the presence of central damselfly predators at 24 °C. Finally, we tentatively tested for the scenario where northern *Daphnia* meet northward moving southern and central damselflies under global warming. The associated contrast (3) compared the relative survival of northern *Daphnia* under two conditions: 20 °C in the presence of northern damselfly predators vs. 24 °C in the presence of northward moving southern and central damselflies. Note that for the interpretation of the latter two contrasts we assume that the relative survival pattern of *Daphnia* from a given latitude does not depend on the presence of northern *Daphnia* (contrast 2) and southern and central *Daphnia* (contrast 3).

## Results

### Damselfly foraging rates

Overall, damselfly foraging rates expressed per individual predator were higher at 24 °C compared to 20 °C (ANCOVA, temperature:  $F_{1,106} = 10.35$ ,  $P < 0.0001$ ; covariates: *Daphnia* size:  $F_{1,106} = 6.91$ ,  $P = 0.0099$ , number of surviving *Daphnia*:  $F_{1,106} = 357.82$ ,  $P < 0.0001$ ). This temperature effect was similar across latitudes (temperature  $\times$  damselfly latitude:  $F_{2,106} = 0.25$ ,  $P = 0.78$ ) (Fig. 1a). Foraging rates differed between damselfly source latitudes, being highest in larvae from the southern latitude (latitude:  $F_{2,106} = 18.44$ ,  $P < 0.0001$ ). These effects remained when expressing damselfly foraging rates per mg body mass (temperature:  $F_{1,106} = 50.96$ ,



**Fig. 1** Effects of temperature and damselfly source latitude on damselfly predation rates on *Daphnia*. Predation rates are expressed as the number of *Daphnia* killed per hour and per individual predator (a) and per hour and per mg damselfly mass (b). Means are given  $\pm 1$  SE. Numbers above bars represent sample sizes.



$P < 0.0001$ , latitude:  $F_{2,106} = 36.41$ ,  $P < 0.0001$ , temperature  $\times$  damselfly latitude:  $F_{2,106} = 1.18$ ,  $P = 0.31$ , covariates: *Daphnia* size:  $F_{1,106} = 3.02$ ,  $P = 0.085$ , number of surviving *Daphnia*:  $F_{1,106} = 223.77$ ,  $P < 0.0001$ ) (Fig. 1b).

#### Relative survival of *Daphnia* prey

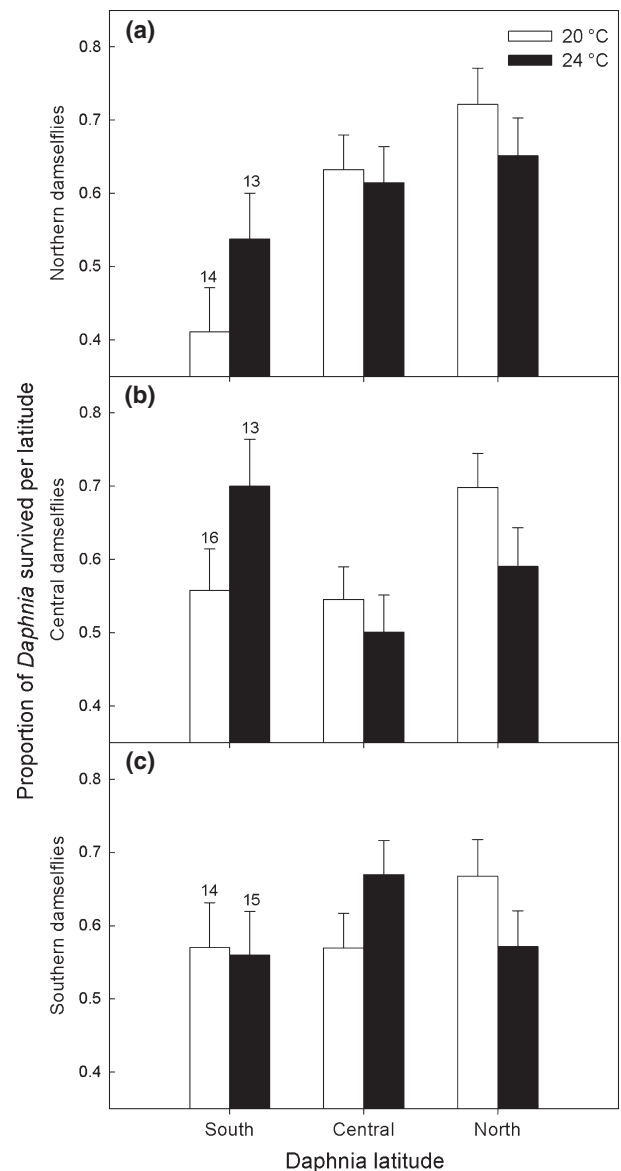
Temperature affected the proportions of *Daphnia* survived from the southern and northern latitudes differently (RM-ANCOVA, temperature  $\times$  *Daphnia* latitude:  $F_{1,78} = 4.96$ ,  $P = 0.029$ , covariate: *Daphnia* size:  $F_{1,78} = 4.66$ ,  $P = 0.034$ ) (Fig. 2). Separate ANCOVAs per *Daphnia* latitude showed opposite temperature effects on *Daphnia* survival from the southern and the northern latitudes (South:  $F_{1,78} = 3.11$ ,  $P = 0.082$ , North:  $F_{1,78} = 5.07$ ,  $P = 0.027$ ), whereas temperature had no effect on *Daphnia* survival from the central latitude (Central:  $F_{1,78} = 0.11$ ,  $P = 0.74$ ). The specific a priori contrast analyses showed in more detail that the proportion of *Daphnia* survived from the southern latitude was higher at 24 °C compared to 20 °C with damselfly larvae from the central and northern latitudes ( $F_{1,78} = 4.87$ ,  $P = 0.030$ ), but not with damselfly larvae from the southern latitude ( $F_{1,78} = 0.014$ ,  $P = 0.91$ ). On the contrary, the proportion of *Daphnia* survived from the northern latitude was higher at 20 °C compared to 24 °C with damselfly larvae from the southern and central latitudes ( $F_{1,78} = 4.32$ ,  $P = 0.041$ ), but not significantly so with damselfly larvae from the northern latitude ( $F_{1,78} = 0.95$ ,  $P = 0.33$ ).

Contrast analyses assuming northward movements of *Daphnia* prey, but not of damselfly predators at 24 °C showed that there were no differences in the relative survival of northern *Daphnia* vs. southern and central *Daphnia* when preyed upon by northern damselfly larvae (contrast,  $F_{1,78} = 0.90$ ,  $P = 0.35$ , Fig. 2a). Yet, the proportion of *Daphnia* surviving from the southern latitude was higher than that from the central latitude (contrast,  $F_{1,78} = 4.06$ ,  $P = 0.047$ ) when preyed upon by central damselfly larvae at 24 °C (Fig. 2b). Compared to the situation at 20 °C in the presence of northern damselfly predators, the proportion of northern *Daphnia* surviving decreased at 24 °C in the presence of southern and central damselfly predators (contrast,  $F_{1,78} = 5.24$ ,  $P = 0.025$ ) (Fig. 2).

## Discussion

#### Local adaptation and thermal plasticity

*Ischnura* damselfly predators from different latitudes differed in foraging rates consistent with a pattern of local latitudinal adaptation to time constraints. Specifically, foraging rates were highest in larvae from the



**Fig. 2** Effects of temperature and damselfly source latitude on the relative survival of *Daphnia* to predation. Relative prey survival is expressed as the proportion of *Daphnia* surviving per source latitude. Means are given  $\pm 1$  SE. Data were arcsin(sqrt) transformed. Numbers above bars represent sample sizes.

southern populations (see also Stoks *et al.*, 2012). This latitudinal difference can be explained by the higher number of generations in the southern populations (two to three per year) compared to the northern populations (one generation per 2 years) (Corbet *et al.*, 2006). This generates a shorter growth period per generation, hence a higher time pressure on the southern populations to grow and develop fast. Indeed, growth rates being fastest and development times shortest in southern larvae have been shown before (Fig. S1, Shama *et al.*, 2011; Stoks *et al.*, 2012).

The observation that northern damselflies had higher foraging rates (this study) and higher growth rates (Shama *et al.*, 2011; Stoks & De Block, 2011; Stoks *et al.*, 2012) at 24 °C than at 20 °C adds to the insight at the interspecies level that thermal optima are often higher than environmental temperatures (Deutsch *et al.*, 2008). This may be linked to the hotter-is-better hypothesis (Kingsolver, 2009), which states that performance will be lower at low temperatures due to thermodynamic constraints. It may therefore pay to evolve higher foraging and growth rates at higher temperatures than the ones normally encountered: even short exposures to higher temperatures will allow significant gains.

The survival of *Daphnia* prey from a given latitude relative to *Daphnia* from other latitudes depended upon the interplay of temperature and the latitude of the predator consistent with a scenario of local thermal adaptation. Relative survival in predator–prey interactions was for southern *Daphnia* higher at 24 °C than at 20 °C and for northern *Daphnia* higher at 20 °C than at 24 °C, indicating local thermal adaptation of the *Daphnia* prey. Yet, this thermal advantage disappeared when they were confronted with the damselfly predators of the same latitude, reflecting also a signal of local thermal adaptation in the damselfly predators. So far, no other studies looked at combined patterns of local thermal adaptation of predators and prey shaping predator–prey interactions along latitudinal gradients. In predator–prey systems where both predator and prey are ectothermic such combined adaptation patterns are likely common, and may shape the effects of global warming (see below).

#### *Possible effects of global warming assuming no dispersal*

Two important, related insights with regard to global warming in closed systems without dispersal arise. First, our data suggest that the predicted temperature increase of 4 °C may strongly increase predation rates at high latitudes and hence be favorable for northern *Ischnura* damselfly larvae. The current intraspecific study thereby complements the interspecies pattern in insects that species at high latitudes are currently living at environmental temperatures cooler than their optimal temperatures, such that climate warming may enhance their fitness (Deutsch *et al.*, 2008). Second, the observation that damselfly foraging rates increase at 24 °C in northern populations directly implies that predation pressures on local *D. magna* will increase. Given that outdoor mesocosm studies indicate that *I. elegans* larvae are capable of causing local extinctions of *D. magna* populations in the absence of fish (Verreydt *et al.*, in prep.), all else staying equal, this may translate into increased extinction probabilities of

*Daphnia* populations in fishless ponds. As *Ischnura* larvae differentially prey on different zooplankton species, this also has the potential to alter zooplankton community composition (Hunt & Swift, 2010). Note that in Thompson's (1978) study of this predator–prey species pair the temperature effect was much stronger at temperatures below 20 °C in penultimate instars, indicating that the expected impact of a 4 °C temperature increase on damselfly foraging rates and the associated predation pressure on *D. magna* may be even larger than based on our results.

#### *Possible effects of global warming in open systems with dispersal*

The observed signals of local adaptation in both predators and prey may inform about effects of global warming in open systems that would not have been revealed using heating experiments with predators and prey from a single latitude. First, comparisons of foraging rates (and growth rates, Stoks *et al.*, 2012) at 24 °C predicts latitude-specific invasion success of northward moving damselflies. The higher foraging rates of southern compared to central damselflies may translate in central populations being outcompeted by southern invaders, although this may not be the case when central populations invade the northern latitude given the similar foraging rates of central and northern damselflies. Note, however, that factors such as the lower cold resistance of the southern damselflies (Stoks & De Block, 2011) may currently limit their northward movements.

Second, comparisons of relative survival at 24 °C tentatively suggest that, all else being equal, latitude-specific invasion success of northward moving *Daphnia*. Central and southern *Daphnia* when invading northern ponds have the same relative survival as local northern *Daphnia* toward northern damselfly larvae. Yet, southern *Daphnia* invading central ponds had a higher relative survival in the presence of central damselfly larvae compared to the local central *Daphnia*, which may promote their invasion success in central ponds. Third, our data tentatively suggest that the change in relative survival of northern *Daphnia* under global warming may depend upon whether or not southern and central damselfly predators invade northern ponds. Indeed, compared to the situation mimicking current conditions (20 °C and northern damselfly predators, but see note below), the relative survival of northern *Daphnia* under global warming did not significantly decrease in the presence of northern damselfly predators, but significantly decreased when confronted with southern and central damselflies. Importantly, these predictions make two assumptions. (1) When comparing the

relative survival of *Daphnia* from a certain set of two latitudes we assume this comparison does not depend upon the presence of *Daphnia* from the third latitude (in our predation trials we always combined *Daphnia* from the three latitudes). (2) We assume that there are no rapid evolutionary responses of local *Daphnia* populations upon warming. Yet, such rapid evolutionary responses have been reported in earlier studies (Van Doorslaer *et al.*, 2009a,b). In more general terms, we may formulate that the strategy of, for instance, the southern *Daphnia* to cope with predation by central damselfly populations under a scenario of global warming is superior to that of the current central *Daphnia* populations. The prediction thus is that the strategy of the central *Daphnia* populations may be replaced by that of the southern *Daphnia* populations, either through invasion of these genotypes or through genetic tracking fueled by genetic variation in the central populations (see De Meester *et al.*, 2011; Urban *et al.*, 2012a).

### Perspectives

There is accumulating evidence that warming can modify existing predator–prey interactions both directly (Gilman *et al.*, 2010; Traill *et al.*, 2010) and indirectly, for example through generating mismatches in the phenology of predator and prey (Winder & Schindler, 2004; Yang & Rudolf, 2010), which may scale up into changes in the strength of trophic cascades (Barton *et al.*, 2009; Kratina *et al.*, 2012). In addition, it is well documented that warming drives range shifts and therefore creates interactions between new combinations of predator and prey species (Gilman *et al.*, 2010). Studies so far, however, largely ignored the latitudinal component of predator–prey interactions (but see Sanford *et al.*, 2003; Laurila *et al.*, 2008; Stoks *et al.*, 2012), and none considered the potential joint local adaptation of predators and prey nor the novel predator–prey interactions between the same predator–prey species pair due to northward movements within species' ranges. Our results highlighted the importance of studying warming effects on predator–prey interactions using both predator and prey populations from different latitudes as temperature effects on relative survival differed across latitudes due to the interplay of local thermal adaptation in both prey and predators. Given that temperature has been shown to affect predator–prey interactions in many species pairs (e.g. through its impact on the functional response; Englund *et al.*, 2011) and local thermal adaptation in predator–prey interactions has been recently documented in another predator–prey system (between spider and grasshoppers; Barton, 2011), our findings likely apply to other predator–prey systems.

Understanding how global warming affects entire communities is a daunting task and the use of community modules, such as the damselfly-zooplankton pair that encapsulates a commonly encountered predator–prey interaction, is an important step toward such challenge (Gilman *et al.*, 2010). The common garden experimental approach using predators and prey obtained from a natural temperature gradient spanning ca. 4 °C and where northern populations are tested at the current and predicted 4 °C temperature increase is a powerful approach to gain mechanistic insights into how community modules will be affected by global warming and can be used as a space-for-time substitution to inform how predator–prey interactions may gradually evolve to long-term warming. As such, this approach complements the field-based approach that integrates experimental and natural gradients to study responses of entire communities and ecosystems (Dunne *et al.*, 2004; Barton, 2011). Although it shares the same limitations of the field-based approach, such as the assumption that animals can adjust to global warming fast enough (Fukami & Wardle, 2005), it generates insights that would not have been revealed from traditional common garden heating experiments at a single latitude. This novel approach may be a valuable addition to the research toolbox including field-based and modeling approaches to arrive at more realistic predictions of global warming effects on the earth's biota (Dunne *et al.*, 2004; Rustad, 2008; Harte & Kueppers, 2012).

### Acknowledgements

We are grateful to Helen Michels, Viktor Nilsson-Örtman, and Karin Rengefors for collecting eggs and to Khuong Dinh Van and Cathy Duvivier for assistance during the experiment. Suggestions by three anonymous reviewers considerably improved the manuscript. MDB and KP are postdoctoral fellows of the Fund for Scientific Research-Flanders (FWO). Financial support came from FWO (G.0419.08 and G.0610.11) and the KU Leuven Research Fund grants GOA/2008/06 and Excellence Center Financing PF/2010/07.

### References

- Abrahams MV, Mangel M, Hedges K (2007) Predator–prey interactions and changing environments: who benefits? *Philosophical Transactions of the Royal Society B-Biological Sciences*, **362**, 2095–2104.
- Araujo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743–753.
- Barton BT (2011) Local adaptation to temperature conserves top-down control in a grassland food web. *Proceedings of the Royal Society B-Biological Sciences*, **278**, 3102–3107.
- Barton BT, Beckerman AP, Schmitz OJ (2009) Climate warming strengthens indirect interactions in an old-field food web. *Ecology*, **90**, 2346–2351.
- Berg MP, Kiers ET, Driessen G *et al.* (2010) Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology*, **16**, 587–598.
- Corbet PS, Suhling F, Soendergerath D (2006) Voltinism of Odonata: a review. *International Journal of Odonatology*, **9**, 1–44.

- De Gelas K, De Meester L (2005) Phylogeography of *Daphnia magna* in Europe. *Molecular Ecology*, **14**, 753–764.
- De Meester L, Van Doorslaer W, Geerts A, Orsini L, Stoks R (2011) Thermal genetic adaptation in the water flea *Daphnia* and its impact: an evolving metacommunity approach. *Integrative and Comparative Biology*, **51**, 703–718.
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 6668–6672.
- Dunne JA, Saleska SR, Fischer ML, Harte J (2004) Integrating experimental and gradient methods in ecological climate change research. *Ecology*, **85**, 904–916.
- Englund G, Ohlund G, Hein CL, Diehl S (2011) Temperature dependence of the functional response. *Ecology Letters*, **14**, 914–921.
- Fukami T, Wardle DA (2005) Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 2105–2115.
- Gilman SE, Urban MC, Tewksbury JJ, Gilchrist GW, Holt RD (2010) A framework for community interactions under climate change. *Trends in Ecology and Evolution*, **25**, 325–331.
- Gosden TP, Stoks R, Svensson EI (2011) Range limits, large-scale biogeographic variation, and localized evolutionary dynamics in a polymorphic damselfly. *Biological Journal of the Linnean Society*, **102**, 775–785.
- Harte J, Kueppers L (2012) Insight from integration. *Nature*, **485**, 449–449.
- Hassall C, Thompson DJ (2008) The effects of environmental warming on Odonata: a review. *International Journal of Odonatology*, **11**, 131–153.
- Hassall C, Thompson DJ (2010) Accounting for recorder effect in the detection of range shifts from historical data. *Methods in Ecology and Evolution*, **1**, 343–350.
- 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.
- Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56–61.
- Hunt RJ, Swift MC (2010) Predation by larval damselflies on cladocerans. *Journal of Freshwater Ecology*, **25**, 345–351.
- IPCC (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, (eds Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE). Cambridge University Press, Cambridge, UK.
- Johnson DM (1991) Behavioral ecology of larval dragonflies and damselflies. *Trends in Ecology and Evolution*, **6**, 8–13.
- Kingsolver JG (2009) The well-tempered biologist. *The American Naturalist*, **174**, 755–768.
- Kratina P, Greig HS, Thompson PL, Carvalho-Pereira TSA, Shurin JB (2012) Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology*, **93**, 1421–1430.
- Laurila A, Lindgren B, Laugen AT (2008) Antipredator defenses along a latitudinal gradient in *Rana temporaria*. *Ecology*, **89**, 1399–1413.
- McPeck MA (1998) The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecological Monographs*, **68**, 1–23.
- Miner BE, De Meester L, Pfrender ME, Lampert W, Hairston NG (2012) Linking genes to communities and ecosystems: *daphnia* as an ecogenomic model. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 1873–1882.
- Parnesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology and Systematics*, **37**, 637–669.
- Parnesan C, Ryrholm N, Stefanescu C *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.
- Rinke K, Vijverberg J (2005) A model approach to evaluate the effect of temperature and food concentration on individual life-history and population dynamics of *Daphnia*. *Ecological Modelling*, **186**, 326–344.
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.
- Rustad LE (2008) The response of terrestrial ecosystems to global climate change: towards an integrated approach. *Science of the Total Environment*, **404**, 222–235.
- Sanford E, Roth MS, Johns GC, Wares JP, Somero GN (2003) Local selection and latitudinal variation in a marine predator–prey interaction. *Science*, **300**, 1135–1137.
- Shama LNS, Campero-Paz M, Wegner KM, De Block M, Stoks R (2011) Latitudinal and voltinism compensation shape thermal reaction norms for growth rate. *Molecular Ecology*, **20**, 2929–2941.
- Stoks R, De Block M (2011) Rapid growth reduces cold resistance: Evidence from latitudinal variation in growth rate, cold resistance and stress proteins. *PLoS ONE*, **6**, e16935.
- Stoks S, Swillen I, De Block M (2012) Behaviour and physiology shape the growth accelerations associated with predation risk, high temperatures and southern latitudes in *Ischnura* damselfly larvae. *Journal of Animal Ecology*, **81**, 1034–1040.
- Thompson DJ (1978) Towards a realistic predator–prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, *Ischnura elegans*. *Journal of Animal Ecology*, **47**, 757–767.
- Traill LW, Lim MLM, Sodhi NS, Bradshaw CJA (2010) Mechanisms driving change: altered species interactions and ecosystem function through global warming. *Journal of Animal Ecology*, **79**, 937–947.
- Urban MC, De Meester L, Vellend M, Stoks R, Vanoverbeke J (2012a) A crucial step toward realism: Responses to climate change from an evolving metacommunity perspective. *Evolutionary Applications*, **5**, 154–167.
- Urban MC, Tewksbury JJ, Sheldon KS (2012b) On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 2072–2080.
- Van Doorslaer W, Stoks R, Duvivier C, Bednarska A, De Meester L (2009a) Population dynamics determine genetic adaptation to temperature in *Daphnia*. *Evolution*, **63**, 1867–1878.
- Van Doorslaer W, Vanoverbeke J, Duvivier C *et al.* (2009b) Local adaptation to higher temperatures reduces immigration success of genotypes from a warmer region in the water flea *Daphnia*. *Global Change Biology*, **15**, 3046–3055.
- Wellborn GA, Skelly DK, Werner EE (1996) Community structure across a freshwater habitat gradient. *Annual Reviews of Ecology, Systematics and Evolution*, **27**, 337–363.
- Wernberg T, Smale DA, Thomsen MS (2012) A decade of climate change experiments on marine organisms: procedures, patterns and problems. *Global Change Biology*, **18**, 1491–1498.
- Winder M, Schindler DE (2004) Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology*, **85**, 2100–2106.
- Woodward G, Perkins DM, Brown LE (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **365**, 2093–2106.
- Yang LH, Rudolf VHW (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters*, **13**, 1–10.
- Young JPW (1979) Enzyme polymorphism and cyclic parthenogenesis in *Daphnia magna*. I. Selection and clonal diversity. *Genetics*, **92**, 953–970.
- Zarnetske PL, Skelly DK, Urban MC (2012) Biotic multipliers of climate change. *Science*, **336**, 1516–1518.

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

- Data S1.** Motivation experimental temperatures.
- Data S2.** Allozyme genotyping of the surviving *Daphnia*.
- Data S3.** Age and mass of the damselfly predators.
- Data S4.** Size of the *Daphnia* prey.