

Thermal acclimation modulates the impacts of temperature and enrichment on trophic interaction strengths and population dynamics

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Abstract

Global change affects individual phenotypes and biotic interactions, which can have cascading effects up to the ecosystem level. However, the role of environmentally induced phenotypic plasticity in species interactions is poorly understood, leaving a substantial gap in our knowledge of the impacts of global change on ecosystems. Using a cladoceran–dragonfly system, we experimentally investigated the effects of thermal acclimation, acute temperature change and enrichment on predator functional response and metabolic rate. Using our experimental data, we next parameterized a population dynamics model to determine the consequences of these effects on trophic interaction strength and food-chain stability. We found that (1) predation and metabolic rates of the dragonfly larvae increase with acute warming, (2) warm-acclimated larvae have a higher maximum predation rate than cold-acclimated ones, and (3) long-term interaction strength increases with enrichment but decreases with both acclimation and acute temperatures. Overall, our experimental results show that thermal acclimation can buffer negative impacts of environmental change on predators and increase food-web stability and persistence. We conclude that the effect of acclimation and, more generally, phenotypic plasticity on trophic interactions should not be overlooked if we aim to understand the effects of climate change and enrichment on species interaction strength and food-web stability.

Keywords: biodiversity loss, climate change, consumer–resource, functional response, metabolic ecology, nonlinear interaction strength, thermal acclimation

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Introduction

Human activities induce rapid environmental changes that pose a major threat to global biodiversity and ecosystem functioning (Pereira *et al.*, 2010). A crucial challenge is therefore to identify conditions and mechanisms that allow species and entire biota to persist and adapt to such changes. Recent studies suggest that evolutionary responses are unlikely to rescue species from deteriorating environmental conditions because they are not fast enough (Quintero & Wiens, 2013). Instead, accumulating evidence indicates that phenotypic plasticity plays a crucial role in the response and adaptation of species to environmental changes (Chevin *et al.*, 2010; Donelson *et al.*, 2011; Munday *et al.*, 2013). Phenotypic responses to environmental changes are indeed common (Huey *et al.*, 2012), can be transmitted between generations (Donelson *et al.*, 2011), and modulate individual physiology, morphology and behaviour to cope with change (Donelson *et al.*, 2011; Forster *et al.*, 2012; Huey *et al.*, 2012). Nevertheless, as prior studies

focused mainly on individual species, the ecological consequences of phenotypic responses to environmental change for species interactions and ecological communities remain largely unexplored (Gilman *et al.*, 2010; Yang & Rudolf, 2010).

Predicting the effects of global warming and other environmental changes on ecological communities is a complex task because species are embedded within communities and their fate depends the consequences of changes in the nature and strength of intraspecific and interspecific interactions (Petchey *et al.*, 1999; Tylianakis *et al.*, 2008; Gilbert *et al.*, 2014). Facing this complexity, ecologists have been developing a mechanistic framework to identify key processes underlying temperature effects on trophic interactions and characterize the impact of global warming on food webs (Binzer *et al.*, 2012; Burnside *et al.*, 2014; Fussmann *et al.*, 2014; Gilbert *et al.*, 2014; Sentis *et al.*, 2014). This framework currently predicts that, over short timescales, warming may destabilize community dynamics by increasing feeding rates. At the same time, metabolic rates often increase faster with temperature than feeding rates (Vucic-Pestic *et al.*, 2011; Fussmann *et al.*, 2014; Iles, 2014). Consumers are thereby less energetically efficient at

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higher temperatures which reduces energy flow between trophic levels and hence stabilizes food-web dynamics in the long run (Binzer *et al.*, 2012; Fussmann *et al.*, 2014; Gilbert *et al.*, 2014). However, if temperature further increases, metabolic demands may exceed ingestion rates and thereby lead to consumer starvation and, ultimately, extinction (Petchey *et al.*, 1999; Rall *et al.*, 2010; Fussmann *et al.*, 2014). Altogether, these results demonstrate that investigating the relative scaling of biological rates with temperature is of paramount importance for predicting ecosystem response to climate change.

Increased eutrophication of terrestrial and aquatic habitats represents another widespread consequence of human activities (Sala *et al.*, 2000). Increased resource availability (hereafter: enrichment) and climate warming may jointly affect food-web stability and structure (O'Connor *et al.*, 2009; Binzer *et al.*, 2012; Sentis *et al.*, 2014). Enrichment increases energy flux from resources to higher trophic levels, which may lead to the paradox of enrichment, that is the higher population fluctuations have a destabilizing effect and lead to increased risk of extinction when population minima are close to or below extinction boundaries (Rosenzweig, 1971; Boukal *et al.*, 2007; Rip & McCann, 2011; Gilbert *et al.*, 2014). Interestingly, moderate warming may alleviate the paradox of enrichment by decreasing consumer energetic efficiency as described above and by lowering resource carrying capacity (Binzer *et al.*, 2012). On the other hand, moderate enrichment increases resource densities and hence reduces consumer starvation risk driven by warming (Binzer *et al.*, 2012). This shows that the combined effects of enrichment and temperature are nonlinear and should be considered explicitly in climate change studies.

The mechanistic framework and results described above have already improved our ability to understand and predict the effects of temperature and enrichment on food webs. However, the response rates (e.g. metabolic and consumption rates) measured or used in these studies originate mainly from short-term experiments in which exposure time to the new thermal environment is often too short to allow for phenotypic response and acclimation (see references in Rall *et al.*, 2012 for examples). As a result, these empirical results and food-web models mostly rely on thermal performance curves (TPCs) describing the effects of acute temperature change on biological rates. However, climate change is an ongoing, gradual process that allows acclimation or phenotypic plasticity to occur (Berg & Ellers, 2010; Donelson *et al.*, 2011). These acclimatory responses can significantly modify the shape and position of the TPCs (Schulte *et al.*, 2011) and consequently alter predictions based

on acute temperature effects (Grigaltchik *et al.*, 2012). Surprisingly, the links between thermal acclimation, acute and chronic temperature change, and trophic interactions remain largely unexplored, leaving a substantial gap in our understanding on how and when acclimation could modulate the consequences of global changes on trophic interactions and food-web dynamics.

The aim of this study was therefore to bridge the gap between studies focused on individual species phenotypic responses to global warming and food-web studies not considering phenotypic plasticity. Using a cladoceran–dragonfly larvae system, we first experimentally investigated the effects of acute temperature change on the functional response and metabolic rate of ‘warm’ and ‘cold’ acclimated predators. Next, we used our empirical results to parameterize a population dynamics model and determine how thermal acclimation modulates the effects of acute temperature and enrichment on trophic interaction strength and food-chain stability.

Material and methods

The experimental system consisted of the larvae of the dragonfly *Sympetrum vulgatum* (Odonata: Libellulidae) preying on *Daphnia magna* (Cladocera: Daphniidae). *Sympetrum vulgatum* is widespread in Europe, and its larvae are important predators in small standing waters, readily preying on *Daphnia* (Klečka & Boukal, 2013).

A colony of *Daphnia magna*, established from individuals collected in a pond near České Budějovice, Czech Republic, was maintained on green algae *Chlorella vulgaris* (Chlorellales: Chlorellales) at 20 ± 2 °C under a 17L:7D photoperiod. *S. vulgatum* larvae of the F-3 (third before last) instar were collected in May 2013 in a small pond near the village of Hospříz (45°07'N, 15°05'E), Czech Republic. In the laboratory, larvae were individually reared in plastic cups (diameter 4 cm, height 10 cm) containing 105 ml of aged tap water and a piece of willow moss, *Fontinalis antipyretica* (Hypnales: Fontinalaceae). Larvae ($n = 190$ per acclimation treatment) were exposed to two contrasting regimes of acclimation temperature, 17.5 ± 0.5 °C and 21.5 ± 0.5 °C (based on continuous measurements using Ebro© EBI 20 units). The regime of 17.5 °C corresponds to the water temperature at the locality when dragonfly larvae were collected and 21.5 °C matches the increase of 4 °C predicted for 2100 (IPCC, 2013). Larvae were fed daily *ad libitum* with *Daphnia* until they reached the last larval instar (hereafter F-0). To account for the effect of temperature on developmental rates, larvae reared at 21.5 and 17.5 °C were, respectively, assayed 5 and 8 days after moulting, which corresponds to ~30% of the developmental time for the last instar at both temperatures (A. Sentis, J. Morisson and D.S. Boukal, unpublished data). *S. vulgatum* larvae were fed *ad libitum* with *Daphnia* and not starved before the experiments. At the onset of all experiments, *S. vulgatum* larvae were allowed to equilibrate to the test temperature for 45 min.

To quantify the *S. vulgatum* functional response (i.e. the relationship between resource density and feeding rate), we used a full factorial design with the two acclimation temperatures (17.5 and 21.5 °C: ‘ambient’ and ‘warm’, respectively) and two acute test temperatures (17.5 and 21.5 °C). This gives a total of four temperature regimes coded as A-17.5, A-21.5, W-17.5 and W-21.5. Experimental arenas consisted of plastic jars (length 7.5 cm, width 5.0 cm, height 10.5 cm) filled with 370 ml of aged tap water. A piece of *F. antipyretica* moss was added in each arena to provide a perching site for *S. vulgatum*. Prey were standardized by age (juveniles 5–7 days old) and body size (mean \pm SE: $18.7 \times 10^{-5} \pm 2.01 \times 10^{-5}$ g wet mass). Prey densities were 5, 10, 20, 40, 70, 100 and 140 *D. magna* per arena (i.e. 13–378 ind L⁻¹), which spans the range of *Daphnia* densities found in Central Europe water bodies (M. Šorf, personal communication). Prey were introduced in the experimental arenas and allowed to acclimate to the test temperatures for 15 h before the start of the experiment. One *S. vulgatum* larva was then introduced in each arena and allowed to feed on *Daphnia* under continuous light conditions. Surviving prey were counted after 7 h to establish prey mortality. Natural mortality of *D. magna* was assessed in control treatments without predators. Ten replicates per each treatment were performed.

Metabolic rates of *S. vulgatum* larvae were measured with an O₂ Microsensor (Unisense©, Aarhus, Denmark) probe coupled to SensorTrace Basic v3.2.3 (Unisense©) software. As in the functional response experiment, we used a full factorial design with two acclimation temperatures (17.5 and 21.5 °C: ‘ambient’ and ‘warm’, respectively) and two acute test temperatures (17.5 and 21.5 °C). Respiration was measured in sealed glass chambers (ca. 57 ml in volume) filled with distilled water, conditioned by added purified salt (Sera©, 0.14 g L⁻¹) to achieve the conductivity of 200 μ S cm⁻¹ that is within the range found in natural habitats of *S. vulgatum* and *D. magna*. Oxygen concentration in each glass chamber was measured just before the introduction of a single *S. vulgatum* larva, and the chamber was then immediately sealed with a glass plug. After 150 min, water in each chamber was mixed using a magnetic stirrer and oxygen concentration measured again. Each larva was then weighed to the nearest 0.0001 g using a Kern© ABT microbalance. A total of 24 replicates per treatment were performed. Possible background oxygen depletion was determined in 10 controls without larvae in each temperature.

Statistical analyses and modelling

All data were analysed using R software, version 2.13.1 (R Development Core Team, 2013).

Functional response

Following standard procedures (Juliano, 2001), a logistic regression between the proportion of prey eaten and initial prey density was performed to discriminate between type II and type III functional responses in each temperature regime. The proportion of prey consumed was positively density

dependent, suggesting a type III functional response. We thereby used the type III Rogers’s random predator equation (Rogers, 1972), which accounts for prey depletion during the time course of the experiment:

$$N_e = N_0(1 - \exp(-bN_0(t - hN_e))) \quad (1)$$

where N_e is the number of prey eaten, N_0 is the initial density of prey (ind arena⁻¹), t is the total experimental time (day), h is the prey handling time (day ind⁻¹), and b is the search coefficient (arena day⁻¹ ind⁻¹) which describes the linear increase in search rate a (arena day⁻¹) with prey density: $a = bN_0$.

To determine the effects of acclimation and acute test temperatures on functional response parameters (b and h), we considered different functional response models covering all possible combinations of temperature dependence in each parameter: b and/or h may depend on acclimation temperature, acute test temperature, both temperatures or neither. This yielded a total of 16 (=2⁴) candidate models that were fitted to the data using a maximum likelihood method and the package ‘bbmle’ (Bolker, 2008). We ranked the models according to their AICc values [Akaike Information Criterion corrected for small sample size (Burnham & Anderson, 2002)] and used parameter estimates from the best-fitting model to calculate consumer energetic efficiency and interaction strength as described below. Data were not corrected for natural *D. magna* mortality in these analyses because mortality in the controls was negligible.

Metabolic rates

The effects of larval body weight, acclimation and acute test temperature on metabolic rates (J h⁻¹) were analysed with an ANCOVA; the analysis included all pairwise interactions of the three explanatory variables. Oxygen depletion in the controls was negligible, and we thus used raw data in the analyses.

Long-term interaction strength

For each temperature regime, we calculated long-term interaction strengths using a standard model of predator–prey dynamics (Yodzis & Innes, 1992):

$$\begin{aligned} \frac{dN}{dt} &= rN \left(1 - \frac{N}{K}\right) - \frac{bN^2P}{bhN^2 + 1} \\ \frac{dP}{dt} &= \frac{e_c bN^2P}{bhN^2 + 1} - cm_p P \end{aligned} \quad (2)$$

where t is time (days), N and P are prey and predator densities (ind L⁻¹), K is the carrying capacity of the prey in the absence of the predator (ind L⁻¹), m_p is the metabolic rate of the predator (J h⁻¹), c converts the metabolic rate to predator individuals per day (J⁻¹ h ind day⁻¹), and e_c (7.39×10^{-4}) is the factor converting consumed prey into predator individuals: $e_c =$ predator assimilation efficiency (0.84 for dragonfly larvae, Corbet, 2004) \times (mean prey body mass) \times (mean predator body mass)⁻¹. We assumed type III functional response with parameters b and h corresponding to our empirical estimates. Following recent studies (e.g. Binzer *et al.*, 2012;

Fussmann *et al.*, 2014), prey intrinsic growth rate r (per day) was calculated as follows:

$$r = r_0 w^{b_r} \exp(-E_r/(kT)) \quad (3)$$

where r_0 is a normalization constant independent of body size and temperature ($11.66 \times 10^{13} \text{ day}^{-1}$ (Savage *et al.*, 2004), w is the prey mass (in μg), b_r is an allometric exponent (-0.25), E_r is the activation energy for invertebrates (-0.84 eV ; Savage *et al.*, 2004), k is the Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$), and T is the environmental temperature (K). Similarly, we assumed that the carrying capacity depends on temperature and resource body mass as follows:

$$K = K_0 w^{b_K} \exp(-E_K/(kT)) \quad (4)$$

where b_K is an allometric exponent (-0.25 ; Fussmann *et al.*, 2014), E_K is the activation energy for invertebrates (-0.77 eV ; Fussmann *et al.*, 2014), and K_0 is a normalization constant independent of body size and temperature. However, the temperature dependence of carrying capacity assumed in Eqn (4) may not always hold; it is still debated whether carrying capacity is most likely to be temperature independent or increase exponentially with temperature (Dell *et al.*, 2013; Gilbert *et al.*, 2014). We therefore investigated the consequences of temperature-independent carrying capacity by setting $E_K = 0$ in Eqn (4) as well. Following the approach of Binzer *et al.* (2012), we varied the intercept K_0 from 0 to 10 as an increasing level of enrichment. This corresponds to the range of prey carrying capacity between 0 and 300 ind L^{-1} , which matches *Daphnia* densities in our experiment and in mesotrophic to eutrophic water bodies in Central Europe (M. Šorf & J. Vrba, personal communication).

We characterized the long-term *per capita* interaction strength I_L using the dynamic index that calculates the log-ratio interaction strength (Berlow *et al.*, 1999; Rall *et al.*, 2010) from the predator-free equilibrium (N, P) = ($N^-, 0$) and the predator-prey equilibrium (N, P) = (N^+, P^+) as

$$I_L = \left| \frac{\ln(N^+/N^-)}{P^+} \right|. \quad (5)$$

In our case, the equilibria obtained by setting the left-hand side in Eqn (2) to zero and solving for N and P are given by $N^- = K$ and

$$N^+ = \sqrt{\frac{cm_p}{b(e_c - cm_ph)}}, \quad (6)$$

$$P^+ = \frac{e_c r}{bK(e_c - cm_ph)} \left(K \sqrt{\frac{b(e_c - cm_ph)}{cm_p}} - 1 \right).$$

To assess the sensitivity of long-term interaction strength to parameters uncertainty, we calculated the 95% CIs of long-term interaction strength by propagating the standard errors associated with the estimates of each experimental parameter (search coefficient, handling time and metabolic rate) using the law of propagation of uncertainty (Rice, 2007) and the 'propagate' package (Spiess, 2014).

Results

We first summarize all our experimental results and subsequently integrate the results on long-term interaction

strength in the context of our modelling framework. In our experiment, *S. vulgatum* larvae did not exhibit the temperature-size rule, that is their body mass was not affected by acclimation temperature ($|t| = 0.23$, $df = 81.6$, $P = 0.82$). Their overall mean (\pm SE) fresh body weight ($0.215 \pm 0.002 \text{ g}$) was thereby used in the calculations of predator and prey equilibrium densities and long-term interaction strengths as outlined below.

Temperature dependence of the functional response

For each temperature regime, prey consumption increased sigmoidally with prey density and maximum feeding rate increased with both acclimation and acute test temperatures (Fig. 1). The data were best described by a model in which acclimation temperature significantly influenced search coefficient and handling time, whereas acute test temperature only affected handling time (Table S1). Larvae acclimated at $17.5 \text{ }^\circ\text{C}$ had a higher search coefficient than those acclimated at $21.5 \text{ }^\circ\text{C}$ (Fig. 2a and Table S2). Handling time decreased with both acclimation and acute test temperatures (Fig. 2b and Table S2): larvae acclimated and tested at $17.5 \text{ }^\circ\text{C}$ (A-17.5) had a longer handling time and lower maximum predation rate compared to larvae acclimated and tested at $21.5 \text{ }^\circ\text{C}$ (W-17.5) (Figs 2b and 3).

Temperature dependence of metabolic rate

Metabolic rate of *S. vulgatum* increased significantly with acute test temperature ($F_{1,84} = 30.16$, $P < 0.0001$; Fig. 4), but was not affected by body mass ($F_{1,84} = 1.76$, $P = 0.19$), acclimation temperature ($F_{1,84} = 0.96$, $P = 0.33$) or the interactions between body mass and test temperature ($F_{1,84} = 0.48$, $P = 0.49$), between body mass and acclimation temperature ($F_{1,84} = 2.68$, $P = 0.11$) and between acclimation and acute test temperature ($F_{1,84} = 0.01$, $P = 0.99$). Removing body mass from the analyses did not qualitatively change the effects of acclimation and test temperature on metabolic rates (analyses not shown).

Predator-prey dynamics and long-term interaction strength

Below the minimum levels of enrichment required for predator persistence, prey reached their carrying capacity (Fig. S1). Above these minimum levels of enrichment (i.e. prey carrying capacity), prey equilibrium densities were independent of enrichment while predator equilibrium densities increased towards a plateau. Overall, prey and predator equilibrium densities increased with both acclimation and acute test temperatures (Fig. S1). Long-term interaction strength increased

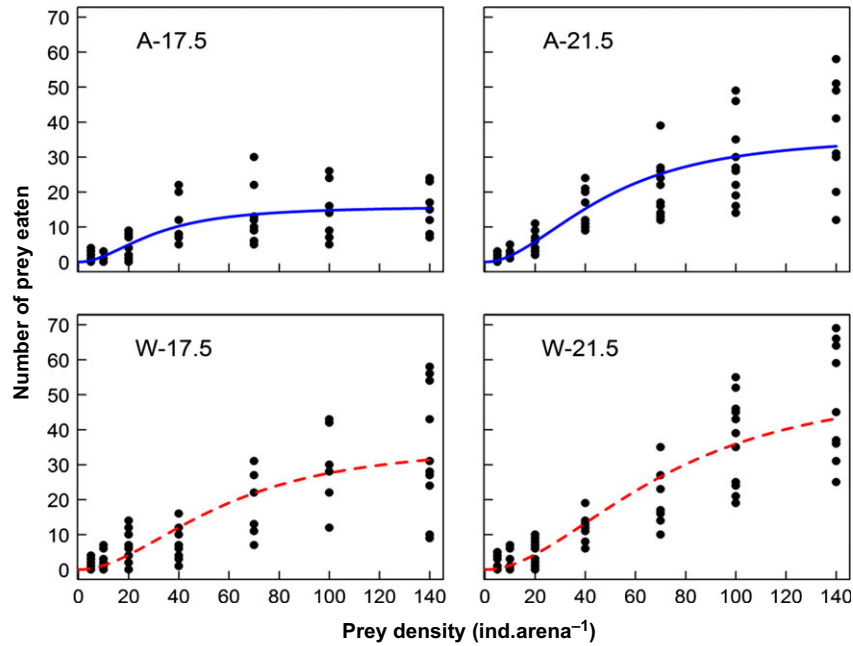


Fig. 1 Functional response of *Sympetrum vulgatum* preying on *Daphnia magna* at two acclimation (17.5 and 21.5 °C: 'A' and 'W', respectively) and two acute test (17.5 and 21.5 °C) temperatures. Sample sizes are $n = 68, 70, 65$ and 68 for A-17.5, A-21.5, W-17.5 and W-21.5, respectively.

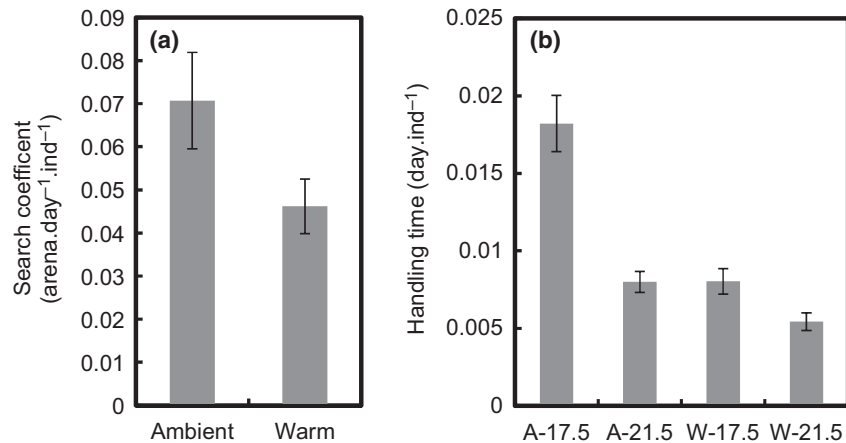


Fig. 2 Functional response parameter estimates (\pm SE) for *Sympetrum vulgatum* preying on *Daphnia magna*. (a) Effect of acclimation temperature (ambient and warm) on the search coefficient b (arena day⁻¹ ind⁻¹). (b) Effects of acclimation (17.5 and 21.5 °C: 'A' and 'W', respectively) and acute test temperatures (17.5 and 21.5 °C) on handling time h (day ind⁻¹). Parameters were estimated from the best-fitting model according to Δ AICc (see Supplementary Information, Tables S1 and S2).

with enrichment but decreased with both acute test and acclimation temperatures although this acclimation effect was only significant at warmer temperature (Fig. 5). As a result, long-term interactions were strongest for predators acclimated and tested at 17.5 °C and weakest for predators acclimated and tested at 21.5 °C (Fig. 5). This result was qualitatively similar when carrying capacity does not depend on temperature (i.e. $E_K = 0$ in Eqn (4); Fig. S2).

Discussion

Understanding how biological rates and species interactions scale with temperature and enrichment is crucial to predict the consequences of environmental change on ecological communities. So far, most experimental and theoretical studies focusing on the effects of acute temperature change on trophic interactions neglected the possibility that phenotypic plasticity may

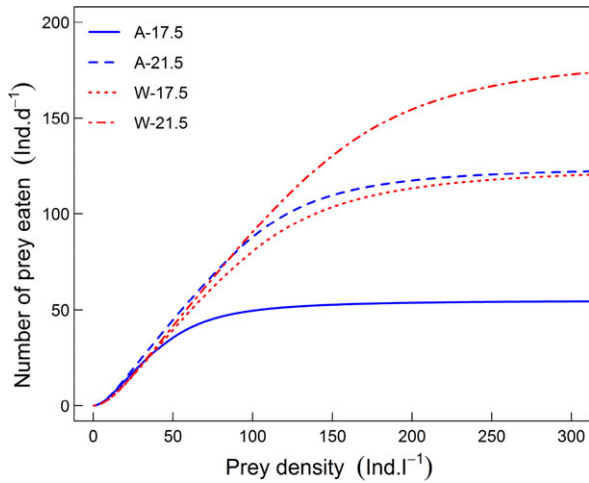


Fig. 3 Functional response curves for *Sympetrum vulgatum* preying on *Daphnia magna* at two acclimation temperature (ambient: A, warm: W) and two acute test temperature (17.5 and 21.5 °C). Curves were generated using type III Rogers's random predator equation (Eqn 1) and parameters estimated from the best-fitting model (see Fig. 2 and Supplementary Information, Table S1 for details).

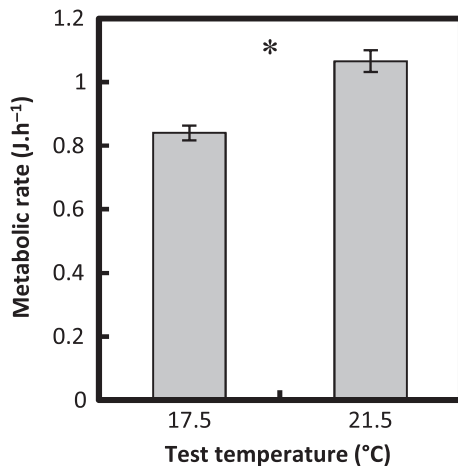


Fig. 4 Effect of acute test temperature on the metabolic rate (Mean \pm SE) of *Sympetrum vulgatum*. '*' Indicates significant differences ($P < 0.05$) between temperature regimes.

modulate these effects. On the other hand, studies on global change and phenotypic plasticity mainly focused on individual species and omitted species interactions. Here, we show, for the first time, that thermal acclimation can strongly alter predator functional response and trophic interaction strengths. By combining experimental and modelling approaches, we identify mechanisms by which thermal acclimation modulate the effects of temperature and enrichment on trophic interaction strength and population dynamics. Our results have several implications for the stability and persistence of food webs, as discussed below.

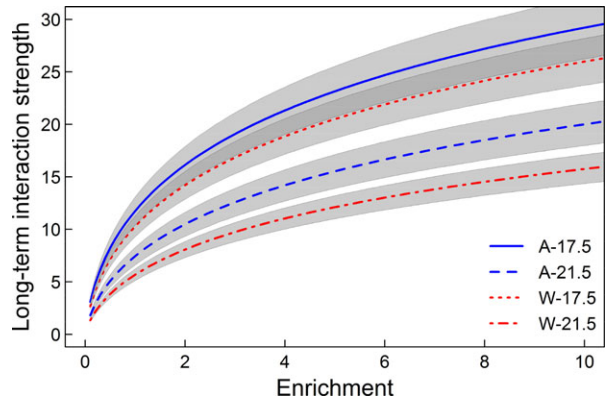


Fig. 5 Effect of enrichment (given by parameter K_0), acclimation (ambient: A, warm: W) and acute test temperature (17.5 and 21.5 °C) on long-term predator–prey interaction strength. Grey bands represent 95% CI intervals, and darker grey indicates their overlap.

Functional response shape

For each temperature regime, we found a type III functional response in which the search rate increases linearly with prey density. In simple predator–prey systems, the shape of the functional response depends on experimental conditions (Hassell *et al.*, 1977), predator–prey size ratio (Kalinkat *et al.*, 2013), prey aggregative behaviour and spatial refuges (Hassell *et al.*, 1977; Akre & Johnson, 1979) and the link between predator searching efforts and prey density (Hassell *et al.*, 1977), which can be influenced by the predator's hunger level (Beukema, 1968; Akre & Johnson, 1979; Mills, 1982). For instance, predators search less for prey at low encounter frequencies (i.e. low prey densities) and this decrease is stronger for satiated predators than for starved ones (Akre & Johnson, 1979). In our study, predators were fully satiated before the experiment, which may explain our results. This hypothesis is supported by another experiment with a slightly different setting in which we assayed starved *S. vulgatum* larvae and found a type II functional response (A. Sentis, J. Morisson and D.S. Boukal, unpublished data). However, we cannot identify the mechanism yielding a type III functional response in this study as the importance of hunger in functional response shapes is not fully understood (Mills, 1982).

Temperature-dependent foraging, metabolism and short-term interaction strengths

In simple predator–prey systems, acute warming generally increases predation rate because predators are more efficient at searching and handling prey (Englund *et al.*, 2011; Rall *et al.*, 2012; Sentis *et al.*, 2012). However,

there is considerable variation in how steeply searching efficiency (i.e. search rate) increases with temperature (Englund *et al.*, 2011; Rall *et al.*, 2012). Recent empirical and theoretical studies suggest that this variation depends on predator–prey relative velocity (Dell *et al.*, 2013; Novich *et al.*, 2014). In ectotherms, velocity increases exponentially with temperature, which leads to higher encounter probabilities and capture rates when predators are active foragers (Sentis *et al.*, 2012; Dell *et al.*, 2013). However, as ‘sit-and-wait’ predators are mostly immobile, temperature has little or no direct effect on their search rate (Dell *et al.*, 2013; Novich *et al.*, 2014; Seifert *et al.*, 2014). In the present study, we used a sit-and-wait predator and found no dependence of search rate on acute temperature in line with the studies mentioned above. The increase in predation rates in our experiment thus stems from the decrease of handling time with acute warming, as ectotherm predators handle and digest prey faster at higher temperatures (Sentis *et al.*, 2013). As a consequence, we found that acute warming increases short-term interaction strength (i.e. predation rate) only at higher resource densities when predation rate is limited by handling and digestion.

A striking result of our study is that thermal acclimation can modulate the effects of acute temperature on both search rate and handling time. Warm-acclimated predators had shorter handling times but were less efficient at searching for prey than ambient-acclimated predators. As a consequence, feeding rates were lower and short-term interactions weaker at low resource densities in warm-acclimated predators than in ambient-acclimated predators, and this relationship was reversed at high prey densities. Our results therefore reveal that thermal acclimation can affect functional response parameters differentially and lead to previously unreported alterations of short-term interaction strengths. Because the functional response is a central component of food-web models and their predictions are sensitive to parameter values, we argue that taking predator and prey thermal history into account in the design and interpretation of functional response experiments is needed to improve our understanding of climate change effects on trophic interactions.

Metabolic rate increased with acute warming, but was not affected by acclimation temperature. Previous studies showed that the magnitude and strength of thermal acclimation effect on metabolic rate varies and depends on species identity, cold and warm thermal acclimation thresholds, and the level of thermal stress experienced during acclimation (Chown *et al.*, 2010; Marshall & McQuaid, 2011; Schulte *et al.*, 2011). It is thereby possible that *S. vulgatum* larvae do not modulate their metabolic rate or that the temperature increase of 4 °C predicted by climatic models (IPCC,

2013) was not large enough to induce measurable changes in this species.

Consequences for individual energy budgets

Changes in feeding and metabolic rates translate into a temperature-dependent energetic efficiency (i.e. *per capita* feeding rate relative to metabolism), which determines the energy available for growth and reproduction and is therefore crucial for individual fitness and population dynamics (Gilbert *et al.*, 2014). Prior studies reported that energetic efficiency can either increase or decrease with acute warming (Rall *et al.*, 2010; Sentis *et al.*, 2012; Iles, 2014) depending on the current temperature, the degree of warming and the shape of the thermal performance curve for a given organism (Sentis *et al.*, 2012). Here, we found that thermal acclimation can subsequently influence energetic efficiency by increasing energy intake at high resource density: warm-acclimated predators have a higher maximum feeding rate than ambient-acclimated predators. That is, thermal acclimation can significantly modify the predictions of previous studies examining the effects of acute temperature on energetic efficiency (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011; Lemoine & Burkepille, 2012; Sentis *et al.*, 2012; Iles, 2014). If prey density is not limiting, we predict that thermal acclimation will increase energetic efficiency and thereby decrease the starvation risk predicted by studies based on acute temperature effects (e.g. Rall *et al.*, 2010; Binzer *et al.*, 2012; Iles, 2014).

At present we cannot extend these conclusions fully to situations in which prey density is limiting, because we have measured the metabolic rate in individually reared and satiated predators. Metabolic rate can vary with food intake rate (Verity, 1985; Schmoker & Hernández-León, 2003) and population density, ostensibly due to food limitation (DeLong *et al.*, 2014). However, joint effects of acclimation and food conditions on metabolic rates and individual energy budgets are entirely unexplored; our results indicate that this question deserves further study.

Consequences for long-term interaction strengths

We found that long-term interaction strengths increase with prey carrying capacity. As described in the Introduction, this makes the predator–prey system more vulnerable to the paradox of enrichment and extinctions (Rosenzweig, 1971; Boukal *et al.*, 2007; Rip & McCann, 2011). On the other hand, we found that acute warming weakens long-term interaction strength and may thus alleviate the paradox of enrichment, as demonstrated by Binzer *et al.* (2012). Interestingly, the stabilizing effect of acute warming on interaction strength

was more pronounced in warm-acclimated predators, suggesting that it could be stronger than previously predicted (Rall *et al.*, 2010; Binzer *et al.*, 2012; Fussmann *et al.*, 2014). While our measure of long-term interaction strength assumes a static predator–prey equilibrium, our results likely hold even when the enrichment leads to predator–prey cycles because the size of the cycles increases with the unstable predator equilibrium density given by Eqn (6), and the latter correlates positively with long-term interaction strength given by Eqn (5) (details not shown). We therefore conclude that thermal acclimation may not only save predators from extinction caused by warming, but also increase food-web stability and persistence.

To conclude, environmental changes affect both individual phenotypes and species interactions, which may have important cascading effects on ecological communities and ecosystem functioning. However, the links between phenotypic responses to environmental changes and species interactions remain poorly understood. By combining modelling and experimental approaches, we identify important links between thermal acclimation, predator foraging behaviour, interaction strengths and food-web stability. We show that thermal acclimation strongly influences predator functional response and trophic interaction strengths which, in turn, may buffer the destabilizing effects of enrichment and decrease extinction risk driven by acute warming. We thereby argue that predictions based on acute thermal performance curves may only be accurate when temperature changes on much shorter timescales (e.g. during daily temperature fluctuations or abrupt heat waves) than the acclimation of biological traits. When temperature changes slowly or acclimation occurs rapidly, the ensuing phenotypic responses must be taken into account to accurately predict the consequences of chronic temperature change on species interactions and community dynamics.

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Supporting Information

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

Figure S1. Effect of enrichment (given by parameter K_0), acclimation temperature (ambient: A, warm: W) and acute test temperature (17.5 and 21.5 °C) on long-term equilibrium densities of (a) prey and (b) predators.

Figure S2. Effect of enrichment (given by parameter K_0), acclimation (ambient: A, warm: W) and acute test temperature (17.5 and 21.5 °C) on long-term predator–prey interaction strength when carrying capacity does not depend on temperature (i.e. $E_K = 0$ in Eqn 4).

Table S1. Summary of the ranking of all candidate models based on different assumption on temperature dependence of the prey search coefficient and handling time.

Table S2. Estimations of *Sympetrum vulgatum* functional response parameters (Mean \pm SE and 95% CI) using the best fitting model (see Table S1 and main text for details).