

Competitive interactions modify the temperature dependence of damselfly growth rates

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Abstract. Individual growth rates and survival are major determinants of individual fitness, population size structure, and community dynamics. The relationships between growth rate, survival, and temperature may thus be important for predicting biological responses to climate change. Although it is well known that growth rates and survival are affected by competition and predation in addition to temperature, the combined effect of these factors on growth rates, survival, and size structure has rarely been investigated simultaneously in the same ecological system. To address this question, we conducted experiments on the larvae of two species of damselflies and determined the temperature dependence of growth rate, survival, and cohort size structure under three scenarios of increasing ecological complexity: no competition, intraspecific competition, and interspecific competition. In one species, the relationship between growth rate and temperature became steeper in the presence of competitors, whereas that of survival remained unchanged. In the other species, the relationship between growth rate and temperature was unaffected by competitive interactions, but survival was greatly reduced at high temperatures in the presence of interspecific competitors. The combined effect of competitive interactions and temperature on cohort size structure differed from the effects of these factors in isolation. Together, these findings suggest that it will be challenging to scale up information from single-species laboratory studies to the population and community level.

Key words: activation energy; Arrhenius equation; cannibalism; Coenagrion; damselflies; exploitation competition; interference competition; intraguild predation; microcosm experiment; size structure; thermal performance.

INTRODUCTION

Climate change is currently having a major impact on the earth's ecosystems (Walther et al. 2002, Parmesan 2006). Much progress has been made in documenting and predicting the effect of climate change on individual species (Parmesan and Yohe 2003, Guisan and Thuiller 2005, Menzel et al. 2006). But species are embedded in complex communities in nature, and shifts in the abundance and competitive ability of different species are among the most pervasive consequences of recent climate change (Tylianakis et al. 2008). Such changes can affect ecosystem functioning (Hillebrand et al. 2008) and may be the single most important factor causing climate-related extinctions (Cahill et al. 2012). A more sophisticated framework that incorporates species interactions is clearly needed and is rapidly emerging (Gilman et al. 2010, Montoya and Raffaelli 2010, Estrela et al. 2012, Lang et al. 2012, Molnár et al. 2013)

Growth rate is one of the most important life history variables, strongly affecting fitness, interactions between organisms, and community dynamics (Binzer et al. 2012). Patterns of individual growth determine the size structure of populations, a factor with considerable importance for determining ecosystem function, food web topology, and regulating trophic cascades (Persson and De Roos 2006, Rudolf 2007a, Brose et al. 2012). Since growth rates are strongly affected by temperature (Angilletta et al. 2004), it is important to know how temperature-dependent growth scales with intra- and interspecific interactions in order to predict community responses to climate change (Brose et al. 2012). Biological interactions that affect growth rates include, but are not limited to, intra- and interspecific exploitation and interference competition, cannibalism, and intraguild predation (Roff 2002). Exploitation competition occurs when individuals (or species) compete for the same resources, and has been shown to be temperature dependent (Davis et al. 1998). Interference competition is also known to depend on temperature (Oyugi et al. 2012), and occurs when one individual (or species) prevents the other from exploiting a shared resource, for example through aggressive behaviors directed toward

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intruders (Oyugi et al. 2012). Finally, cannibalism, the consumption of conspecifics, and intraguild predation, the killing and consumption of potential competitors, have also been shown to be temperature dependent (Crumrine 2010, Reglero et al. 2011). Because these interactions occur between individuals that compete for a shared resource, we will refer to them collectively as competitive interactions. Noncompetitive interactions, such as predation by individuals that do not overlap in resource use, may potentially also affect growth rates. But in this study our focus will lie on the first four types of competitive interactions. Few studies have investigated all these four processes in relation to growth and temperature within the same system.

In addition to affecting individual growth rates, competitive interactions also affect the size structure of populations (Persson and De Roos 2006). This occurs, for example, through size-dependent cannibalism, where some individuals gain rapidly in size at the expense of reduced growth rates in others (McPeck 2004). This can result in bimodal size distributions (Claessen et al. 2004) and cohort splitting in organisms with complex life cycles (e.g., when part of a cohort displays a one-year life cycle and the other a two-year life cycle) (Johansson and Norling 1994). The joint effect of temperature and competition on the size distribution within cohorts is a neglected issue in our understanding of ecological temperature effects.

Metabolic scaling theory (Brown et al. 2004) has recently emerged as the standard approach to model temperature-dependent biological processes (such as growth rates) in predictive climate change models (Vasseur and McCann 2005, Montoya and Raffaelli 2010, Woodward et al. 2010, Molnár et al. 2013). According to this framework, the rate of biological processes (for example growth rate) increases exponentially with temperature at temperatures below the thermal optima according to Boltzmann-Arrhenius equation

$$R = b_0 e^{-E/kT} \quad (1)$$

where R is the rate, b_0 is an organism-dependent scaling factor, E is the activation energy (in electron volts [eV]), k is Boltzmann's constant (8.62×10^{-5} eV/K) and T is the temperature in Kelvin (Brown et al. 2004). The parameter E here describes the slope of the relationship between biological rates and temperature (at the "Arrhenius scale" of $-1/kT$), and represents the parameter of greatest interest for climate change research (Woodward et al. 2010). Although metabolic scaling theory is contested (Clarke 2004, Glazier 2005, O'Connor et al. 2007), the Boltzmann-Arrhenius equation provides a reasonable empirical approximation of how temperature affects the average trait value of many biological traits (Gillooly et al. 2001, Savage et al. 2004, Irlich et al. 2009, Knies and Kingsolver 2010, Dell et al. 2011). Based on how intra- and interspecific interactions may modify growth rates and size structure, caution is

clearly needed when scaling up information on temperature-dependent processes from laboratory studies to the ecosystem level. In addition, current climate change models based on metabolic scaling do not incorporate trait variance or population size structure (Brose et al. 2012).

We here study two species of damselflies in the Temperate Zone genus *Coenagrion*, the Central European *C. pulchellum* and the North European *C. armatum*. These species were chosen because they are known to differ in the temperature dependence of growth rates (Nilsson-Örtman et al. 2012, 2013), and because *C. pulchellum* is currently expanding its range northwards into the range of *C. armatum*, likely due to climate change (Hickling et al. 2005). Because the temperature dependence of damselfly growth rates varies consistently across latitudes (Nilsson-Örtman et al. 2013), it represents a promising trait to incorporate into a climate change framework (Sarmiento et al. 2010, Woodward et al. 2010).

We conducted two complementary laboratory experiments designed to test for temperature effects on growth rates, survival and size structure at three levels of ecological complexity. In the first, larvae were reared individually at three temperatures under typical laboratory conditions. In the second experiment, larvae were reared in groups of 30 individuals in microcosms at two temperatures and three species combinations (*C. armatum* only, *C. pulchellum* only, or an equal number of individuals of each species). To aid in the interpretation of the results we estimated and compared the activation energy (E) of growth rates under each of these three scenarios. Our focus lies in testing to what extent rate-temperature relationships (the slope of thermal reaction norms) estimated under controlled laboratory conditions can be used for predicting the climate change responses of species when embedded in a community context, and to test how temperature and competition alter individual patterns of growth, survival, and cohort size structure.

METHODS

Study system

Our study system consists of two damselfly species, *Coenagrion armatum* (dark bluet) and *C. pulchellum* (variable bluet), sampled from natural populations near Sundsvall, North-Central Sweden (62° N). *C. armatum* represents a boreal species restricted to the northeast of Europe, whereas *C. pulchellum* is widespread in Central Europe (Dijkstra and Lewington 2006). The two species are sympatric at the sampled sites, but these lie close to the current northern range margin of *C. pulchellum*. *C. armatum* has recently disappeared from much of its southern range, but it is not known whether this is due to climate change or habitat loss (Sahlén et al. 2004). *C. pulchellum* is rapidly spreading northwards, likely due to climate change (Hickling et al. 2005). Both species emerge and mate in spring (the flight period of both

species spans from mid-May to July). Larval development typically takes two years, with winters being spent in the cold-tolerant larval stage (Johansson and Norling 1994, Corbet et al. 2006). Larval winter diapause is initiated by both low temperatures and short photoperiods (Pritchard 1989). Dragonflies are known to be highly plastic in terms of voltinism, i.e., the number of generations per year (Corbet et al. 2006). Thus, some fast-growing individuals are likely to be able to complete development in one year, and some slow-growing individuals may require three years to finish larval development. This phenomenon is known as cohort-splitting (Johansson and Norling 1994). *Coenagrion* larvae are aquatic predators of smaller invertebrates. Together with other odonate taxa, they are major predators in aquatic ecosystems, contributing greatly to energy turnover (Benke 1976). Interference and exploitation competition as well as intraguild predation and cannibalism is common in coenagrionid damselflies (McPeck and Crowley 1987, Anholt 1990, 1994, Johansson 1993, 1996).

Common garden experiment

This experiment, hereafter referred to as the “common garden experiment,” was carried out between June and November in 2008, 2009, and 2010 to determine the effect of temperature on growth rates, survival, and cohort size structure of damselfly larvae when reared individually under typical laboratory conditions. The experiment consisted of two species (*C. armatum* and *C. pulchellum*) and three temperatures (16°, 19°, and 21°C; see *Temperature considerations* in Appendix A for more details). Each species was represented by 17 family groups, replicated five times (individual larvae) per temperature treatment. The sample size at the start of the experiment was thus 2 species \times 3 temperatures \times 17 families \times 5 replicates = 510 individual larvae. The experiment was carried out in indoor climate chambers in the laboratory in Umeå, Sweden under a fixed 14:10 L:D photoperiod. These data were originally collected as part of a comparative study involving six species (Nilsson-Örtman et al. 2012, 2013). *C. armatum* was collected and reared in 2008 from females collected at Hamstasjön (62°28'5" N, 17°16'38" E), Kråkholmen (62°30'50" N, 17°28'55" E) and Sticksjön (62°24'51" N, 17°16'18" E). *C. pulchellum* was collected and reared in 2009 and 2010 from Bergtjärnen (62°24'34" N, 17°12'57" E), Sticksjön (as previously) and Strömsås (62°31'26" N, 17°9'8" E). All sites are located within a 17-km radius. Females were collected in the field and placed in plastic jars lined with wet filter papers, into which eggs were deposited. After eggs had hatched, 15 full-sib offspring from each family were transferred to individual 100-mL rearing containers, and five offspring were randomly placed in each of three climate chambers set to produce the experimental temperatures. Climate chambers were switched twice during the experiment. Larvae were fed six days a week on *Artemia salina* nauplii (282 ± 62

nauplii [mean \pm SD] based on 25 randomly chosen samples). This corresponds to a food density of ~ 2.8 nauplii/mL. *Coenagrion* individuals were photographed at the age of 0, 42, 84, and 126 days. These photographs were used for size measurements. For size measurements and growth rate calculations, see *Calculating growth rates*. In total, the experiment yielded growth rates of 157 individuals from 17 families of *C. armatum* and 202 individuals from 17 families of *C. pulchellum*, corresponding to 3.07 and 3.96 individuals per combination of family and temperature, respectively.

Microcosm experiment

This experiment, hereafter referred to as the “microcosm experiment,” was carried out between June and November 2010 to determine the effect of temperature on growth rates, survival, and cohort size structure of damselfly larvae when reared in the presence of conspecific or heterospecific competitors. The most important aspects of the experiment are described here (additional details in Appendix A). *Coenagrion* larvae were reared in microcosms in a 2×3 factorial experimental design that included two temperature treatments (16°C and 21°C) and three combinations of damselfly species (*C. armatum* only, *C. pulchellum* only, or both species combined). Each treatment was replicated eight times, resulting in a total of 48 microcosms. Each microcosm contained 30 *Coenagrion* larvae at the start of the experiment, representing a larval density of 300 individuals/m². This corresponds to typical field densities in suitable habitats of related species (Corbet 1999). The sample size at the start of the experiment was thus 3 species combination \times 2 temperatures \times 8 replicates \times 30 larvae = 1440 individual larvae.

Coenagrion larvae used for the experiment were randomly drawn from a sample of 2 ± 1 day old first-instar larvae representing 17 genotypic groups of each species (the same genetic diversity as in the common garden experiment). These clutches came from females that were collected on 9, 10, and 12 June 2011 from Sticksjön and Strömsås, two of the populations that were also used in the common garden experiment. We refer to these as the “source populations.”

Microcosms consisted of round, white, plastic bowls (~ 7 -L volume, diameter 345 mm, height 130 mm) filled with 3L of water, fresh grass, algae, microorganisms and freshwater snails. Each microcosm received a food ration of 4200 ± 1900 *Artemia salina* nauplii (mean \pm SD; based on 30 random samples) six days a week and 200 ± 28 *Daphnia magna* individuals (based on five random samples) twice a week. The experiment was carried out in indoor climate chambers in the laboratory in Umeå, Sweden under a fixed 14:10 L:D photoperiod. Climate chambers were switched twice during the experiment.

The experiment was initiated on 30 June; this will be referred to as day 0 of the experiment. On this day, 30 individuals were randomly drawn from the source

populations and added to each microcosm. For the intraspecific treatments, all 30 individuals were of the same species. For the interspecific treatments, 15 individuals of *C. armatum* and 15 individuals of *C. pulchellum* were introduced into each microcosm. To trace the growth of *Coenagrion* larvae within each microcosm, larvae were monitored on four occasions. On day 0, head widths were measured for about 10 individuals from each included family. On day 42 and 84, a random sample of 10 individuals was taken from each microcosm. On day 126, all microcosms were emptied and all surviving larvae collected. Size measurements and growth rate calculations are described next.

Calculating growth rates

In both experiments, *Coenagrion* individuals were photographed at the age of 0, 42, 84 and 126 days (± 1 day), referred to as “measurement events.” At these days, we took photographs of each individual from a fixed distance against a millimeter scale paper using a Canon 350D digital camera (Canon Europa NV, Amstelveen, The Netherlands) and a Tamron 90mm f2.8 macro lens (Tamron Company, Saitama, Japan). Head width, estimated as the maximum distance between the distal parts of the eyes, was measured from these photographs using ImageJ 1.43 (National Institutes of Health, Bethesda, Maryland, USA). The millimeter paper grid was used for size calibration. Head width is a good approximation of overall size in odonates, displaying less allometric variation than other size measures (Corbet 1999).

Size-corrected relative growth rates (RGRs) were calculated following Rose et al. (2009). Individual growth trajectories were modeled as a third-degree polynomial function of head width, hw , and time, t , of the form

$$\log[1 + hw(t)] = at + bt^2 + ct^3 \quad (2)$$

with a , b , and c being polynomial coefficients estimated from the data. RGRs were calculated as the slope of the fitted curve at the point in time when larvae reach a reference size, L_c . In previous studies, L_c has corresponded to one-fifth the adults' head width of each species (Nilsson-Örtman et al. 2012, 2013). For *C. armatum* and *C. pulchellum*, this corresponds to a head width of 0.77 and 0.81 mm, respectively. In this study, we used $L_c = 0.8$ mm for both species. Varying L_c from 0.6 to 1.2 mm did not affect the final outcome of these analyses.

In the microcosm experiment, it was not feasible to keep track of individual larvae between measurement events. Instead, we used a stratified resampling approach (Tillé 2006) to fit Eq. 2 for “pseudo-individuals,” which we describe. If N is the number of larvae surviving at day 126 in a replicate rearing unit, we resampled with replacement N observations from the original data for this replicate at each measurement event. This yields a

symmetrical data set with $4N$ observations for each replicate. Next, we ranked observations within measurement events by increasing size. Assuming that the smallest individual at day 0 was also the smallest individual at later measurement events, we treated observations with the same rank order (across measurement events) as belonging to the same pseudo-individual. An example of this approach applied to real data for fast- and slow-growing groups of individuals is shown in Appendix B: Fig. B2.

Calculating the activation energy, E

For each experiment, we translated the slope of the rate–temperature relationship into a corresponding activation energy, E , by fitting the OLS regression between $\log(\text{RGR})$ and $-1/kT$ (Hawkins et al. 2007). The slope of this relationship corresponds to the parameter E in Eq. 1. Note, however, that these estimates are based on three temperatures in the common-garden experiment and two temperatures in the microcosm experiment. Because E depends strongly on the number and range of temperatures used to estimate it (Knies and Kingsolver 2010), our estimates of E must be seen as rough approximations and we present them here to ease interpretation of our results. Importantly, estimates of E presented here rely heavily on the assumption that responses are linear at the Arrhenius scale over the experimental temperature range. Based on previously published data from three *Coenagrion* species measured at four temperatures between 16°C and 24°C (Nilsson-Örtman et al. 2013), responses are indeed reasonably linear over the temperature range used here. But again, we would like to emphasize that estimates of E are meant to aid in the interpretation of the magnitude of shifts in the slope of temperature responses by presenting them at a familiar scale.

Data analysis

Each replicate unit was represented by the average size-corrected relative growth rate (RGR) across all individuals. Thus each of the 17 families per species and temperature in the common garden experiment and each of the 8 microcosms per species, treatment, and temperature in the microcosm experiment was represented by a single data point. In order to investigate the temperature dependence of larval growth rates under varying levels of ecological interactions we performed four analyses of variance (ANOVA). In each of these, $\ln(\text{RGR})$ was the dependent variable and temperature (at the scale of $-1/kT$; abbreviations as in Eq. 1) was included as an independent variable.

First, we assessed whether the two species differed in the temperature dependence of growth rates when reared individually. For this, we used data from the common garden experiment and tested for the effects of species and temperature on growth rates in a two-way ANOVA. Second, we assessed whether the two species

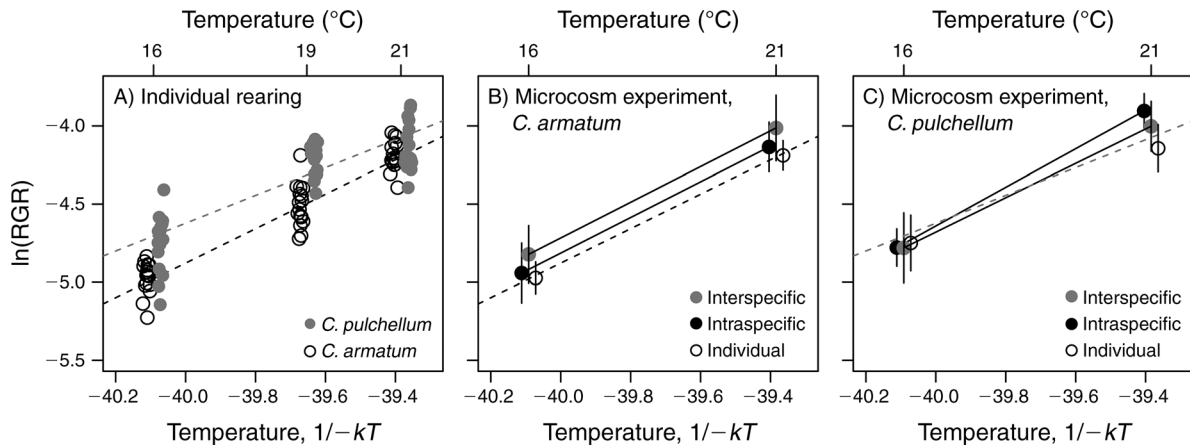


FIG. 1. Rate-temperature relationships of size-corrected growth rates (RGRs) of larval damselflies when reared under varying levels of ecological complexity. Each panel shows the natural logarithm of RGRs plotted against the inverse rearing temperature in kelvins multiplied by the Boltzmann factor. At this scale, the slope corresponds to the activation energy, E (eV). Actual rearing temperatures (in °C) are shown above each plot. Data points have been slightly jittered along the x -axis for clarity. (A) RGR plotted against temperature for larvae reared individually at three temperatures. The slope corresponds to an activation energy of 1.10 ± 0.11 eV (mean and 95% CI) in *Coenagrion armatum* (black dashed line) and 0.89 ± 0.16 eV in *C. pulchellum* (gray dashed line). (B) RGRs of *C. armatum* when reared at two temperatures either individually (open circles), in microcosms with conspecifics (black circles), or in microcosms with heterospecifics (gray circles). (C) RGRs of *C. pulchellum* plotted against temperature for the same three treatments. For ease of interpretation, the dashed lines in (B) and (C) show the activation energy estimated from individually reared larvae at three temperatures in (A).

differed in the temperature dependence of growth rates when reared in the presence of competitors, and if the slope of temperature responses depended on the identity of the competing species. For this, we used data from the microcosm experiment and tested for the effects of species, temperature, and competition type (intraspecific or interspecific) on growth rates in a three-way ANOVA. Because the analyses of the common garden and microcosm experiments revealed contrasting patterns, we performed two additional analyses to explore these differences in greater detail. We combined data from both the common garden and microcosm experiment at 16°C and 21°C and fitted two species-specific ANOVAs, testing for the effects of species, temperature, and rearing method on larval growth rates. Here, rearing method was a factor with three levels: reared individually, with intraspecific competition, or with interspecific competition. In the latter analyses, we identified significant contrast between main effects using Tukey's HSD tests for multiple comparisons, while interaction contrasts, as implemented in the function *testInteractions* in the R package *phia*, were used to identify significant contrasts between factors involved in interactions.

To investigate patterns of larval survival, we performed log-linear analyses testing for the effects of temperature and rearing method (individual, interspecific, or intraspecific) on the percentage of larvae surviving until day 126 in each species. We then tested whether among-replicate variation in residual growth rates (correcting for differences between species and temperatures) co-varied with among-replicate variation in mortality rates. We tested for the interacting effects of

species, temperature, competition type, and mortality rates on residual growth rates in a four-way ANOVA. Continuous input variables were centered at zero and scaled by dividing them by the standard deviation, following Schielzeth (2010).

Temporal changes in the larval size distribution were investigated by calculating the coefficient of variation (CoV) of larval head widths for each measurement event and treatment group separately. Confidence intervals of the coefficients of variation were calculated using Vangel's (1996) modified McKey approach. Tukey's HSD tests were used to assess whether treatment groups differed in average head width at each measurement event. All statistical analyses were performed with R 2.15.2 (R Development Core Team 2012). Raw data from both experiments and R code used to produce Fig. 1 are available in the Supplement.

RESULTS

Growth rate and temperature

In the common garden experiment, size-corrected relative growth rates (RGR) were higher at all temperatures in the Central European *C. pulchellum* than in the North European *C. armatum* (Fig. 1A; Table 1A, species effect). The relationship between growth rate and temperature was steeper in *Coenagrion armatum* than in *C. pulchellum* (Fig. 1A; Table 1A; species \times temperature interaction). The slopes of the growth rate-temperature relationships corresponded to an activation energy, E , of 1.10 ± 0.11 eV (mean and 95% CI) in *C. armatum* and 0.89 ± 0.16 eV in *C. pulchellum* (Fig. 1A).

TABLE 1. Results from the five ANOVAs on the effects of temperature and rearing method on the size-corrected growth rates (RGRs) of damselfly (*Coenagrion*) larvae.

Model and effect	df	MS	F	P
A) Common garden experiment				
Species	1	0.99	48.04	<0.001
Temperature ($-1/kT$)	1	8.38	405.90	<0.001
Species \times temperature	1	0.10	4.65	0.034
Residuals	97	0.02		
B) Microcosm experiment				
Species	1	0.12	4.14	0.047
Temperature ($-1/kT$)	1	10.48	369.36	<0.001
Competition type	1	0.04	1.32	0.256
Species \times temperature	1	0.02	0.68	0.413
Species \times competition type	1	0.13	4.69	0.035
Temperature \times competition type	1	0.04	1.24	0.270
Species \times temperature \times competition type	1	0.00	0.08	0.772
Residuals	56	0.03		
C) <i>C. armatum</i>				
Temperature ($-1/kT$)	1	10.33	680.33	<0.001
Rearing method	2	0.11	7.18	0.002
Temperature \times rearing method	2	0.01	0.55	0.579
Residuals	58	0.02		
D) <i>C. pulchellum</i>				
Temperature ($-1/kT$)	1	8.37	322.25	<0.001
Rearing method	2	0.03	1.25	0.295
Temperature \times rearing method	2	0.10	3.99	0.024
Residuals	61	0.03		

In the microcosm experiment, *C. pulchellum* again grew faster than *C. armatum* at both temperatures (Fig. 1B, C; Table 1B, species effect). However, the slope of temperature responses did not differ between species (Table 1B, nonsignificant species \times temperature interaction) nor did the slope differ consistently between competition treatments (Table 1B, nonsignificant interactions involving temperature and competition type). Pooling data from the intra- and interspecific treatment groups, the slope of temperature responses in the microcosm experiment corresponded to an activation energy of 1.09 ± 0.20 eV in *C. armatum* and 1.11 ± 0.16 eV in *C. pulchellum*. Thus, although the activation energies of growth rates differed significantly between species in the common garden experiment, they were identical in the microcosm experiment.

Analyzing the data for *C. armatum* in greater detail, the slopes of temperature responses were found to be identical regardless of rearing method (Fig. 1B; Table 1C, nonsignificant interaction between temperature and rearing method). Average growth rates differed between treatments (Table 1C, rearing method effect) and a Tukey's HSD analysis revealed that growth rates were significantly higher in the interspecific treatment than in the two other treatment groups ($P < 0.005$) but did not differ between larvae reared individually or with intraspecific competitors ($P = 0.74$). In the detailed analysis of *C. pulchellum* data, the relationship between growth rate and temperature was found to be steeper in larvae reared with intraspecific competitors than in the common garden experiment (Fig. 1C; Table 1D,

significant interaction between temperature and rearing method; Tukey's HSD, intraspecific vs. individual, $P = 0.024$; other contrasts $P > 0.15$). Average growth rates did not differ between treatments in *C. pulchellum* (Table 1D, treatment effect). Thus, the reason that the two species differed in the slope of temperature responses in the common garden experiment but not in the microcosm experiment was that competitive interactions between conspecifics increased the slope of temperature responses in *C. pulchellum* (Table 1C), while competitive interactions had no effect on temperature responses in *C. armatum* (Table 1D).

Survival

In *C. armatum*, survival was higher at 16°C than at 21°C (log-linear analysis, temperature \times survival, $\chi^2_2 = 23.05$, $P < 0.001$), and there was a significant interaction between temperature and rearing method (log-linear analysis, temperature \times rearing method \times survival, $\chi^2_2 = 23.05$, $P < 0.001$; Fig. 2A). These interactions reflected that survival was lower in the interspecific treatment group at 21°C (log-linear analysis at 21°C, treatment \times survival, $\chi^2_2 = 35.29$, $P < 0.001$), but not at 16°C (log-linear analysis at 16°C, treatment \times survival, $\chi^2_2 = 5.16$, $P = 0.076$). In *C. pulchellum*, survival did not depend on temperature (log-linear analysis, temperature \times survival, $\chi^2_1 = 0.04$, $P = 0.850$; temperature \times rearing method \times survival, $\chi^2_2 = 3.10$, $P = 0.213$). Instead, larval survival was higher when reared individually than when reared in the presence of competitors (log-linear analysis, treatment \times survival, $\chi^2_2 = 9.54$, $P = 0.008$). Overall, survival

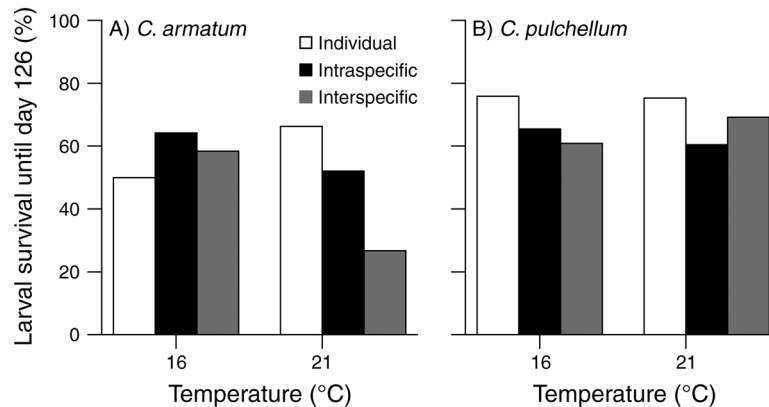


FIG. 2. Larval survival until day 126 (day 0 is 30 June) as a function of species, temperature, and rearing method (individual rearing, with intraspecific competition in microcosms, and with both intra- and interspecific competition in microcosms).

was lower in *C. armatum* than in *C. pulchellum* (Fig. 2A, B; log-linear analysis, species \times survival, $\chi^2_{11} = 26.88$, $P < 0.001$).

Mortality rates did not directly predict the residual variation in growth rates (ANOVA, $\text{RGR} \sim \text{species} \times \text{temperature} + \text{mortality}$, mortality effect, $F_{1,55} = 0.001$, $P = 0.93$). Instead, the final model included a significant temperature \times mortality interaction as well as a significant species \times competition \times mortality interaction (Table 2). A marginally nonsignificant four-way interaction between species \times temperature \times competition \times mortality ($F_{1,48} = 3.28$, $P = 0.076$) was excluded on the basis of AIC scores, and because the predictions from the model that included this interaction (AIC = 75.01) did not differ qualitatively from a model without it (AIC = 73.79). The predictions from the simpler model are shown in Fig. 3. In *C. pulchellum*, growth rates increased with mortality in the intraspecific treatment at 21°C, but displayed a weak negative correlation with mortality in the interspecific treatment group (Fig. 3D). The reversed pattern was observed in *C. armatum* at 21°C (Fig. 3B). Differences between species remained also at 16°C, but the overall effect was less steep than at 21°C (Fig. 3A, B).

Size structure

Individuals in the microcosm experiment showed significantly more variation in head widths than individuals of the same age in the common garden experiment (Fig. 4). In the common garden experiment, the coefficient of variation of head widths increased up to day 42, after which it tended to stabilize at a value of about 0.1 (Fig. 4; open circles). In contrast, variability increased monotonically in both species in the microcosm experiment at 16°C (Fig. 4A, C; filled symbols). At 21°C, variability increased rapidly up to day 84, after which it decreased in both species (Fig. 4B, D; solid symbols), likely because more individuals reached the asymptotic size.

Changes in the size distribution at different points in time are shown in Figs. 5 and Appendix B: Fig. B3. Tukey's HSD analysis revealed that larvae of *C. armatum* reared with intraspecifics were significantly larger than larvae reared individually after 126 days at 16°C (Fig. 5A). In *C. pulchellum*, larvae reared with intraspecifics were significantly larger than individually reared larvae after 42 days at 21°C (Fig. 5D). Comparing individually reared larvae with larvae from the interspecific treatment groups yielded virtually identical results

TABLE 2. Results from a four-way ANOVA on the effects of mortality rate, competition type, temperature, and species on growth rates of damselfly (*Coenagrion*) larvae. See Fig. 4 for an illustration of the significant interaction terms involving mortality.

Effect	df	MS	F	P
Species	1	1.002	6.589	0.013
Temperature	1	50.575	332.593	<0.001
Competition	1	0.07	0.457	0.502
Mortality	1	0.001	0.009	0.925
Species \times temperature	1	0.219	1.439	0.236
Species \times competition	1	0.682	4.485	0.039
Temperature \times competition	1	0.009	0.061	0.805
Species \times mortality	1	0.061	0.404	0.528
Temperature \times mortality	1	0.84	5.525	0.023
Competition \times mortality	1	0.075	0.493	0.486
Species \times competition \times mortality	1	1.558	10.245	0.002
Residuals	52	0.152		

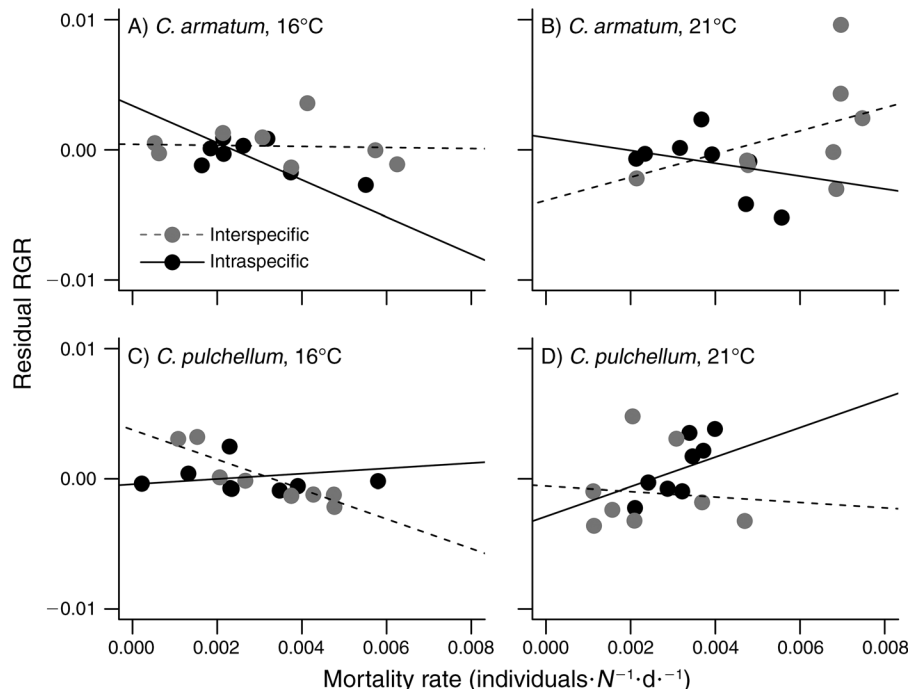


FIG. 3. Effects of mortality on growth rates of damselfly larvae. Each symbol represents one microcosm, with eight replicate microcosms for each combination of species, temperature, and competition treatment. Mortality rates are the per capita mortality rate, i.e., the number of mortalities divided by the initial sample size in each microcosm ($N = 30$ for intraspecific treatment group and $N = 15$ for the interspecific treatment group) divided by the duration of the experiment. Growth rates are represented by the residuals from a two-way ANOVA containing species and temperature as independent variables. Solid and dashed lines show the predicted relationships between growth rate and mortality rate from the model containing a three-way interaction between species \times competition type \times mortality and a two-way interaction between temperature \times mortality. See Table 2 for details of this model.

(not shown), and the only significant difference between the intra- and interspecific treatment groups was that larvae of *C. pulchellum* reared with intraspecifics were significantly larger than larvae reared with interspecifics at day 126 at 21°C (Appendix B: Fig. B3D).

DISCUSSION

Predicting ecological responses to climate change is challenging due to the inherent complexity of species interactions, physiological processes, and the interaction between the two (Gilman et al. 2010, Molnár et al. 2013). Our study both supports and challenges the use of single-individual laboratory experiments for predicting community responses to climate change. Three main observations emerge from this study: (1) that the average growth performance was relatively similar regardless of rearing method; (2) that competitive interactions modified the temperature dependence of growth rates and survival, but that species differed in the strength and direction of these effects; and (3) that the combination of competition and temperature had stronger effects on population size structure than on average growth rates. We will outline each of these issues in some detail in the following paragraphs.

Average growth rates across treatments

If we compare the average head widths at different points in time directly, the similarities between rearing methods are quite striking (Fig. 5 and Appendix B: Fig. B3; solid lines). In terms of average relative growth rates, the rank order of the two species was also unaffected by rearing method: *C. pulchellum* grew faster than *C. armatum* regardless of how they were reared (Fig. 1B, C). Thus, even a highly “unnatural” laboratory experiment yielded reasonably accurate qualitative predictions of the relative growth performance of these two species under more natural conditions. This fits well with several other studies that have found a similar agreement between laboratory and field studies of other aspects of damselfly ecology (Pierce et al. 1985, Baker 1989, Stoks et al. 2005a). Nevertheless, we observed significant differences between species in both growth rates and survival depending on the rearing method used.

Competition and mortality effects on temperature responses

Temperature-specific growth rates differed between rearing methods, with temperature responses differing in both elevation (Fig. 1B, Table 1C) and slope depending

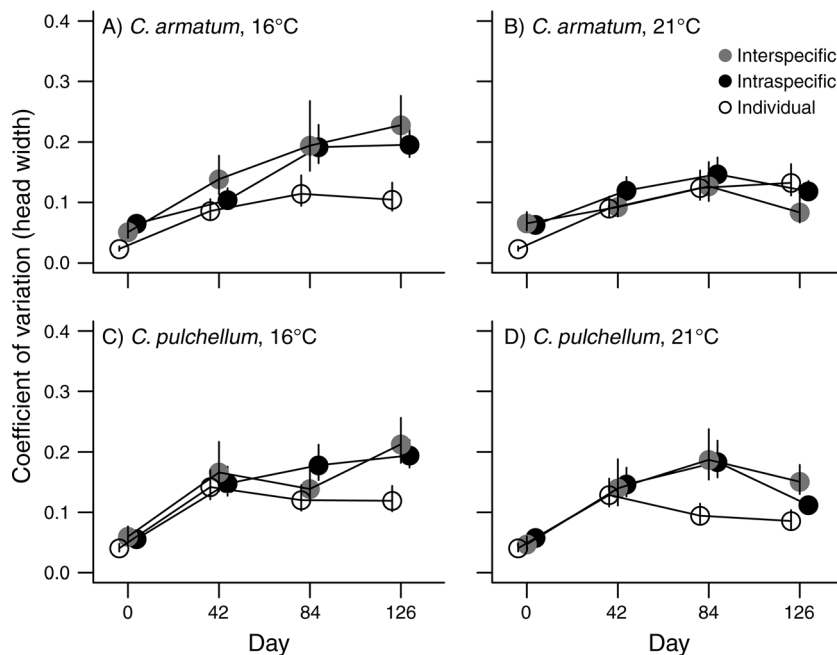


FIG. 4. Size variability (expressed as the coefficient of variation of head widths) of damselfly larvae reared under varying levels of ecological complexity at two temperatures. Results are shown for (A, B) *C. armatum* and (C, D) *C. pulchellum*. The three treatment groups represent larvae reared individually under laboratory conditions (open circles), in microcosms with conspecific competitors (black circles) and in microcosms with both con- and heterospecific competitors (gray circles). Day 0 is 30 June. Error bars show 95% modified McKey confidence intervals of the coefficient of variation (Vangel 1996).

on the ecological context (Fig. 1C, Table 1D). That growth rates are context dependent is not surprising, as growth rates have previously been shown to depend on both competition, predation, and food quality in damselflies as well as in other taxa (Baker 1982, Anholt 1990, Anholt and Werner 1995, McPeck 2004). A novel result was that the slope of temperature responses (i.e., the activation energy, E) was modified by competitive interactions, and that species differed in how strong this effect was. Thus, the slope remained unchanged in the presence of competitors in *C. armatum* (Fig. 1B, Table 1C), but became steeper when *C. pulchellum* was reared with conspecifics (Fig. 1C, Table 1D). The changes in the latter were sufficiently strong that differences in the slope observed between species in the common garden experiment were completely absent in the microcosm experiment. This clearly demonstrates that laboratory estimates of the temperature dependence, E , of ecologically important traits such as growth rates are not directly transferrable to more natural conditions (Gilman et al. 2010, Moenickes et al. 2012). These findings mirror several recent studies that have demonstrated that species-specific differences in behavioral or physiological characteristics can give rise to unexpected changes in species interactions with increasing temperatures (Davis et al. 2002, Lang et al. 2012).

The present study was not designed to tease apart the mechanistic basis for the observed differences in growth rate. Theoretical and empirical evidence suggests that

the higher growth rates in the microcosms can result from either differences in food quality (Scriber and Slansky 1981), size-dependent mortality (Van Buskirk and Yurewicz 1998), or behavioral and physiological trade-offs between individuals' activity levels, feeding rates, and predation risk (McPeck 2004, Stoks et al. 2005a, b, 2012). Since we did not measure behavioral and physiological traits in the present study, we cannot assess their contribution here, but consider it highly likely that the risk of being predated in the microcosms triggered behavioral and physiological responses that affected individuals' growth rates.

Mortality patterns could alter the slope of temperature responses of growth rates if mortality rate increases with temperature and mainly affects smaller individuals (with higher levels of mortality being mirrored in higher apparent growth rates). We found no support for this effect. Instead, mortality rates differed between temperatures in *C. armatum*, but the slope was unaltered by competitive interactions (cf. Figs. 1B, 2A). In *C. pulchellum*, the pattern was reversed: mortality rates did not differ between temperatures, but the slope of temperature responses was altered by competitive interactions (cf. Figs. 1C, 2B). Our analysis of among-replicate variation also did not reveal any clear-cut relationship between mortality and growth rates (Fig. 3). From this we infer that larval mortality was not strongly size dependent in the majority of cases. It is worth noting, however, that we detected a strong, positive

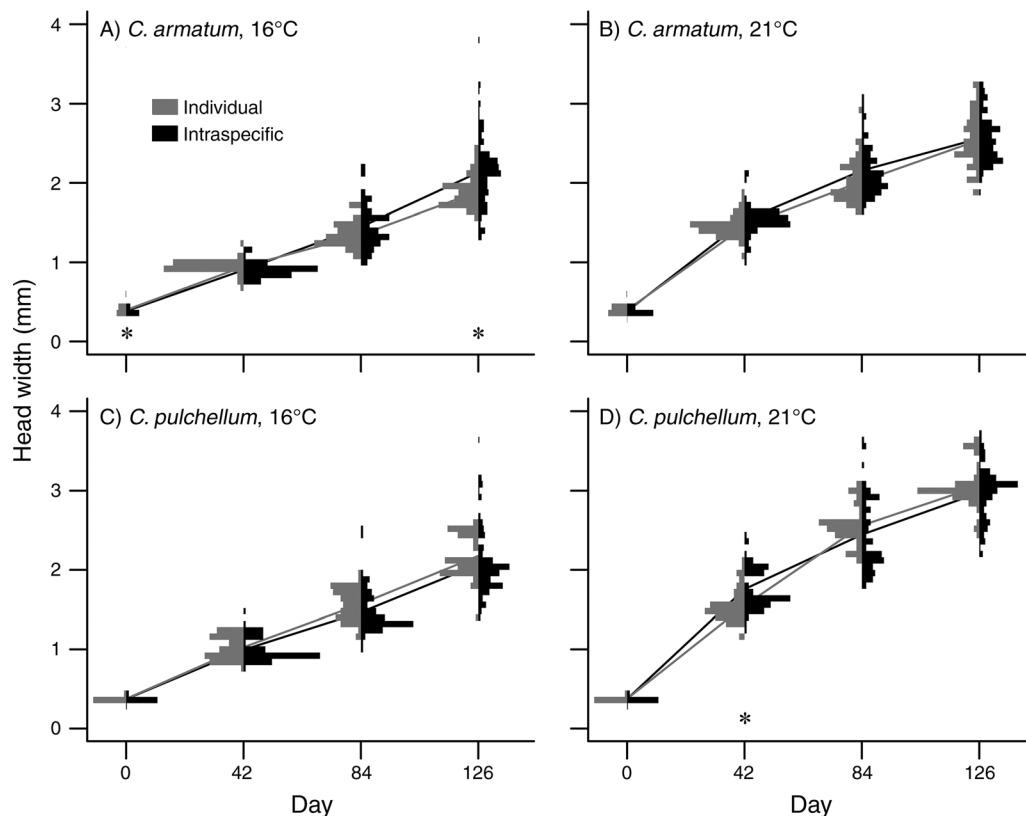


FIG. 5. Changes in the size distribution of cohorts of damselfly larvae reared at two temperatures, either individually (shown in gray) or in microcosms in the presence of conspecific competitors (shown in black). Note that singular, very large individuals are present in both species after 84 days in the microcosms at 16°C (A, C; intraspecific), but not when larvae were reared individually. Black and gray lines join the median value at each point in time. The size distributions of larvae reared in the presence of intra- or interspecific competitors were essentially identical (cf. Appendix B: Fig. B3). Day 0 is 30 June. Asterisks denote significant comparisons ($P < 0.05$) based on Tukey's HSD tests (see Appendix C: Tables C1–C4 for details).

correlation between mortality rates and growth rates in one treatment group: *C. pulchellum* reared with intraspecifics at 21°C (Fig. 3D). This treatment group also displayed greater mortality and higher growth rates than other treatment groups in this species, suggesting that size-dependent cannibalism may have been a major cause of mortality when *C. pulchellum* was reared with conspecifics at the highest temperature, but negligible otherwise. That *C. armatum* suffered substantial mortality in the interspecific treatment at this temperature further corroborates this interpretation, suggesting that individuals of *C. pulchellum* may have been strongly cannibalistic when reared in isolation, but switched to preying heavily on *C. armatum* when this species was present.

Throughout this paper, we have referred to interactions among individuals as competitive interactions because larvae compete for the same food in the microcosms. However, it is not necessary that the present finding hinges on the fact that species compete for a shared resource. Rather, noncompetitive interactions such as predation could also be expected to produce complex changes in temperature responses, for

example, if species differ in how temperature affects components that underlie growth–predation trade-offs or patterns of size-dependent predation, such as activity levels, components of the function response, or food conversion efficiencies (McPeck 2004, Sentis et al. 2013).

Size structure

With respect to cohort size structure, our findings have important consequences for how the results from different experimental designs are interpreted and for how we can predict ecosystem responses to climate change. Intriguingly, larvae displayed considerably greater size variability in the microcosm experiment than in the common garden experiment (Fig. 4). The implications of the observed size variability for ecological response to climate change become clearer when we consider what these size differences mean in terms of the composition of larval instars at the end of the experiment. In damselflies, the final instar prior to emergence is referred to as the F0 instar, with preceding instars being numbered sequentially as F1, F2, and so on. When reared in microcosms at 16°C, two individuals of *C. armatum* and several individuals of *C. pulchellum*

reached the F0 (head width ~ 3.7 mm) instar (Fig. 5A, C; black bars). When reared individually at 16°C , however, neither species reached beyond the F2 (~ 2.2 mm) instar (Fig. 5A, C; gray bars). In addition, even though F0 larvae were present in *C. armatum* when reared in microcosms at 16°C , no individuals of this species reached beyond the F1 instar when reared in microcosms at 21°C (Fig. 5B; black bars), despite that average RGRs were considerably higher at 21°C (Fig. 1B). The existence of singularly fast-growing individuals at 16°C but not at 21°C suggests that individual differences in temperature-specific food intake rates, growth efficiencies, or a combination of both can in some instances compensate for, or completely overcome, the rate-depressing effects of temperature on growth rates (Clarke 2003, Heilmayer et al. 2004; but see Present and Conover 1992, Stoks et al. 2012).

The size differences that we observed in the microcosms are more than sufficient to cause cohort splitting, whereas size differences observed in the common garden experiment are likely to be too small for this to occur (Johansson and Norling 1994). Cohort splitting will effectively double the fitness of fast-growing individuals relative to slow-growing individuals (in terms of the intrinsic rate of increase, r) (Huey and Berrigan 2001, Kingsolver and Huey 2008). In addition, fast-growing individuals will have a disproportionately large influence on intra- and interspecific interactions, since these are strongly dependent on the relative, rather than absolute, size of the interacting individual (Polis et al. 1989, Rudolf 2007b). Thus, although these singularly large individuals are numerically rare, they can have a considerable impact on the community dynamics of these species (Persson and De Roos 2006). Depending on whether models of community responses to climate change include such information on trait variances, and if they are based on growth parameters from experiments with or without competitive interactions, the predictions regarding the outcome of climate change will be very different.

Conclusions

This study demonstrates that species interactions can modify the temperature dependence of ecologically important traits in unexpected ways. In one species, competitive interactions increased the thermal sensitivity of growth rates, whereas in the other, the thermal sensitivity of survival was increased in the presence of interspecific competitors. Two important conclusions can be drawn from these findings. The first is that we cannot view single-species laboratory estimates of the temperature dependence of traits such as growth and survival as reflecting a fundamental physiological property of an organism. Consequently, we urge researchers to be cautious when using such data to predict rates of ecological processes at higher levels of biological organization (e.g., Brown et al. 2004) or ecosystem responses to climate change (e.g., Sarmiento et

al. 2010, Woodward et al. 2010). Instead, we recommend viewing such estimates as a way to generate hypotheses about how organisms respond to changing environmental conditions. These hypotheses must then be rigorously tested using carefully designed experiments such as ours.

Second, our findings highlight the fact that growth and survival represent complex processes that are shaped by many underlying behavioral, physiological, and ecological factors, each of which may differ in their dependence on intra- and interspecific interactions and temperature (McPeck 2004, Stoks et al. 2005b). In order to understand how ecosystems respond to climate change, we must therefore strive to identify the factors that ultimately determine the outcome of species interactions and give rise to variation in individual's performance (Sentis et al. 2013). That competition affected patterns of growth and survival differently in the two species suggests that species-specific differences in growth–predation trade-offs may be an important aspect of how ecosystems respond to climate change. Our findings with respect to cohort size structure also suggest a need to pay considerably more attention to the distribution of trait values. Taken together, it seems inevitable that a unification of physiological and ecological principles across multiple hierarchical levels will require hard work and a joint consideration of multiple physiological, behavioral, and ecological processes.

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SUPPLEMENTAL MATERIAL

Appendix A

Additional details on the microcosm and common garden experiments ([Ecological Archives E095-120-A1](#)).

Appendix B

Supplementary figures showing the larval size distribution at hatching, illustrating how growth rates were calculated in the microcosm experiment using stratified resampling, and a comparison of temporal changes in the size distribution of larvae in the intra- and interspecific treatment groups ([Ecological Archives E095-120-A2](#)).

Appendix C

Tables showing results from Tukey's HSD tests on larval head widths ([Ecological Archives E095-120-A3](#)).

Supplement

Raw data from the common garden and microcosm experiments, and R code for calculating relative growth rates and producing Fig. 1 and Table 2 ([Ecological Archives E095-120-S1](#)).