Austral Ecology (2007) **32**, 766–774 doi:10.1111/j.1442-9993.2007.01758.x

Between-species differences in demographic responses to temperature of coexisting cladocerans

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Abstract In this work we report on the seasonal trends of abundances in terms of temperature exposure for four coexisting cladoceran species (*Daphnia ambigua* (Daphniidae), *Ceriodaphnia dubia* (Daphniidae), *Diaphanosoma chilense* (Sididae) and *Moina micrura* (Moinidae)) from a Chilean temperate lake. In order to compare the demographic response to temperature, we used life table experiments to parameterize matrix models for the four species at four fixed temperatures. From these life table response experiments we assessed the effects of temperature, species and their interaction on the variation in growth rate, as well as the contribution of juvenile survival, adult survival, fertility and age at first reproduction to the changes in growth rate. Our results showed interspecific differences in the effect of temperature on the growth rate. Species that present higher field abundance at lower temperature also exhibited, under controlled experiments, higher growth rates at low temperature and lower growth rates at high temperature, relative to the additive model. Conversely, species with higher abundances during the warmer seasons exhibited higher growth rates at higher experimental temperatures and lower growth rates at lower temperatures, relative to the additive model. The vital rates that most contributed to the variation in growth rate were age at first reproduction and fertility. Our growth rate estimates matched predictions of the metabolic ecology model.

Key words: Chile, *Daphnia*, lake, life table response experiment, matrix model.

INTRODUCTION

Freshwater zooplankton are often exposed to severe changes of biotic and abiotic conditions in their natural habitats that define individual as well as population performance (see Lampert 1987). The source of this variation is a compromise between the temporal changes in the environment and the ability of organisms to move or migrate across the horizontal and vertical dimensions of a heterogeneous space. For example, in many temperate lakes, environmental factors such as temperature, oxygen concentration, photosynthetically active radiation, damaging ultraviolet light, as well as food density and quality often exhibit a strong vertical structure (see Lampert & Sommer 1997). At the same time, these factors often show large temporal fluctuations on a seasonal time scale (Sommer *et al.* 1986). On the other hand, zooplankton are known to perform vertical (Lampert 1989; Reichwaldt & Stibor 2005) as well as horizontal (Siebeck 1980; Burks *et al.* 2002) migrations on an hourly scale.

In this work we were interested in the effects of temperature on the demography of the cladoceran fauna of a temperate Chilean lake (lake El Plateado). This question was motivated by three patterns observed in the system. (i) The lake presents a marked temporal (seasonal) and spatial (vertical) temperature structure (Ramos-Jiliberto *et al.* 1997). (ii) The inhabitant cladoceran species exhibit different seasonal changes in population sizes. Remarkably, the only *Daphnia* species reproduces during the winter (Ramos-Jiliberto *et al.* 1998). (iii) Some of the cladoceran species exhibit significant diel changes in temperature exposition during part of the annual cycle as a consequence of vertical migration behaviour (Ramos-Jiliberto & Zúñiga 2001; Ramos-Jiliberto *et al.* 2004). This scenario can be considered representative of the non-montane lake systems of central Chile and of many temperate monomictic lakes in other parts of the world.

Several studies have established that temperature directly affects instar duration of cladocerans and consequently defines important life history traits such as age at first reproduction and intrinsic population growth rate (Bottrell 1975a,b; Lei & Armitage 1980; Geller 1987; Berberovic *et al.* 1990; Cole *et al.* 2002; Hall & Burns 2002; Lemke & Benke 2003; Vijverberg & Koelewijn 2004; Weetman & Atkinson 2004). Temperature can also indirectly affect the expression of other vital rates as well as population growth. The population dynamics of cladocerans is the result of the realized time-dependent rate of population growth, which is defined by the values of individual-level

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Accepted for publication January 2007.

parameters such as development rate, fertility and survival probability. The development rate of cladocerans of a given body size is mainly governed by temperature, fertility is mainly affected by food consumption and survival is usually controlled by predation. The variation in time and space of these ecological factors will shape the time evolution of population growth. Temperature also affects many physiological rates, including feeding rate and body growth (Burns 1969; Goss & Bunting 1983; Korpelainen 1986). Therefore, population growth rate can also be affected by temperature, within the limits of its reaction norm, via variation in one or more vital rates.

On the other hand, cladoceran mortality through predation in the field is counterbalanced by antipredator traits exhibited by the cladoceran prey. Diel vertical migration constitutes one of the most common behavioural defences exhibited by zooplankton, but the gain in survival is often compromised by reduction in other fitness components, such as development rate and food acquisition (Lampert 1989; De Meester *et al.* 1999). Temperature reduction is considered to be a major source of costs associated with predator avoidance through vertical migration (Dawidowicz & Loose 1992; Loose & Dawidowicz 1994). Therefore, the population dynamics of zooplankton after performing diel vertical migration depends on the reaction norm of migrating zooplankton to environmental temperature.

As there is clear evidence that the cladoceran fauna of our study system exhibit periodic changes in temperature exposure, we evaluated the demographic mechanism by which temperature variation affects the population growth rate of four coexisting cladocerans species, under laboratory-controlled conditions. Although earlier work has shown the importance of temperature for defining vital rates of *Daphnia* and other cladocerans, few experimental studies have simultaneously dealt with a group of coexisting species. As the experimental set-up strongly alters the quantitative estimation of vital rates and life history traits, our approach allowed a comparison of the between-species differences of demographic responses to temperature, by taking advantage of the current techniques embodied in life table response experiments (hereafter LTRE) analyses (Caswell 2001).

We asked three specific questions: (i) Do the differential seasonal trends of population densities translate to differential exposure to temperature in the field? (ii) Do cold-growing species exhibit a relative demographic advantage at low temperature in controlled experiments, while warm-growing species exhibit a relative demographic advantage at higher temperature? and (iii) Which vital rates explain the temperature-driven variation of population growth rates?

METHODS

Field data

The four species studied here inhabit lake El Plateado, which is a small eutrophic and warm-monomictic lake located at 33°04′30″S, 71°39′12″W at 340 m a.s.l. in Valparaíso, Chile. Its surface area is 18 700 m^2 (Domínguez *et al.* 1976), with a maximum depth of 13 m. Chemical and physical characterization of this lake can be found in Domínguez *et al.* (1976, 1981) and Ramos-Jiliberto *et al.* (1997). A strong stratification phase occurs from September to May, with a temperature range of 9–24°C, and gradients up to 6°C m^{-1}. The hypolimnion becomes severely hypoxic during most of the stagnation period (Ramos-Jiliberto *et al.* 1997). Seasonal population changes of the zooplankton were reported in Ramos-Jiliberto *et al.* (1998). Excluding shallow ponds and high-Andean systems, El Plateado shares its main limnological features with most of the lakes in Central Chile.

Data of cladoceran population density were obtained every 2 weeks during a 2-year period by vertical hauls (125 μm mesh), from lake bottom to the surface, at the deepest point of the lake. Our own experience on this lake (Ramos-Jiliberto & Zúñiga 2001; Ramos-Jiliberto *et al.* 2004) indicated that sampling at this point provided a good approximation to the average zooplankton abundance within the pelagic zone. Zooplankton samples were fixed in the field and counted in the laboratory, following standard procedures (McCauley 1984). The temperature of the lake water was measured simultaneously with plankton sampling, using a WTW OXI 196 oxymeter/thermometer and a calibrated WTW EOT 196 submergible probe. For ordination purposes, we defined three epilimnetic temperature ranges: low (<12.5°C), medium (12.5–17.5°C) and high (>17.5°C), measured at 1 m below the surface. In order to test for within-species differences in population density over field temperature ranges we performed Kruskal–Wallis ANOVA by ranks, and multiple comparisons of mean ranks.

Experimental data

A LTRE approach is used here to estimate the demographic responses of four coexisting species under different constant temperatures covering its environmental range. Life tables were run under laboratory conditions, using species *Daphnia ambigua* (Daphniidae), *Ceriodaphnia dubia* (Daphniidae), *Diaphanosoma chilense* (Sididae) and *Moina micrura* (Moinidae) as experimental animals. Individuals of each species were isolated from lake El Plateado and cultured in the

laboratory using filtered lake-water as medium and a culture of *Chlorella* sp. as food, isolated from the same lake.

In order to obtain the experimental individuals, several adult females were randomly isolated from monoclonal cultures and inoculated in individual flasks. Then, all neonates born at the same day were isolated individually and used as same-aged mothers. These mothers were acclimated to the experimental temperature, and newborns (<24 h old) from their third brood were used for constructing the life tables. For each species/temperature combination, 10–12 newborns were put into individual 80 mL beakers, immersed in a temperature-controlled (±0.5°C) water-bath at the following temperatures: 10°C, 15°C, 20°C and 25°C. Every other day, each animal was checked for age-specific maternity (m_x, defined as number of live offspring) and survivorship (being l_x the survival probability to age x). Afterward, the experimental animals were put in fresh medium containing saturating food (20 µg Chlorophyll-a per litre). The food was prepared every other day, and its concentration was calculated from optical density, using a regression curve made for these experiments. In previous experiments made at a single temperature (20°C), we calculated the saturation level of food, and checked that interclonal variation was significantly lower than interspecies variation.

The life tables were run until the third brood per individual was released. Two individuals of the species *D. chilense* and one of *M. micrura* were discarded for analyses since they died shortly after the beginning of the experiment.

Age-structured model

For each species/treatment case, an age-structured matrix model was constructed from survivorship and maternity functions recorded in the life tables. The input coefficients in the projection matrix are the survivorship probabilities (P_i) and fertilities (F_i), obtained according to formulas proposed by Caswell (2001) for birth-flow populations:

$$P_i = \frac{l(i+1) + l(i)}{l(i) + l(i-1)} \tag{1}$$

$$F_i = \frac{(l(0)l(1))^{1/2}}{2}(m_i + P_i m_{i+1}) \tag{2}$$

where $l(i)$ is the survival probability from birth to age i, and $m(i)$ is the brood size at age i.

The population growth rate was calculated as the dominant eigenvalue (λ) of the projection matrix, and the associated right and left eigenvectors give the stage-stable structure (w), and reproductive value (v), respectively.

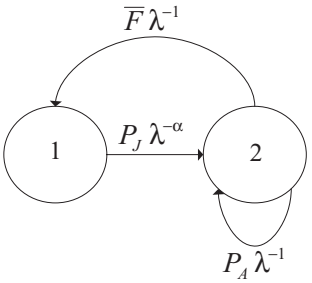

Fig. 1. Two-stage life cycle graph, with transition rates defined by age at maturity α, probability P_J of surviving to maturity, adult survival probability P_A, and fertility $\overline{F}$.

Stage-structured model

From the age-structured matrix we developed a simplified two-stage model with juveniles and adults as state variables (Fig. 1). Here, juveniles survive with probability P_J to reach maturity, spending α time units in the process. The adults survive with probability P_A during one projection interval, that is

$$P_J = \sigma_1^{\alpha} \tag{3}$$

$$P_A = \sigma_2 \tag{4}$$

According to Levin *et al.* (1996), $\alpha = m - 1$ is the number of time steps before reaching maturity. We calculated the age class at maturity m from the individual life tables, as the rounded arithmetic mean of the first age classes with non-zero maternity. This parameterization allows us to capture smaller differences in individual time to maturity, and thus to minimize the information loss involved in the construction of the reduced matrix model from the individual life tables.

P_J was considered as the probability to survive to age class m, i.e. $\prod_{i=1}^{m} P_i$. The adult survivorship (σ_2) and adult fertility ($\overline{F}$) were calculated according to Levin *et al.* (1996) as:

$$\sigma_2 = \frac{\sum_{i=m}^{\infty} w_i P_i}{\sum_{i=m}^{\infty} w_i} \tag{5}$$

$$\overline{F} = \frac{\sum_{i=m}^{\infty} w_i F_i}{\sum_{i=m}^{\infty} w_i} \tag{6}$$

The sensitivities of λ to changes in these parameters were derived from the characteristic equation of the matrix model (Caswell 1996; Levin *et al.* 1996):

$$\frac{\partial\lambda}{\partial\sigma_1} = \frac{\alpha\sigma_1^{\alpha-1}\bar{F}}{(\alpha+1)\lambda^{\alpha} - \sigma_2\alpha\lambda^{\alpha-1}} \quad (7)$$

$$\frac{\partial\lambda}{\partial\sigma_2} = \frac{\lambda}{(\alpha+1)\lambda - \sigma_2\alpha} \quad (8)$$

$$\frac{\partial\lambda}{\partial\alpha} = \frac{-\lambda^{\alpha+1}\log\lambda + \sigma_2\lambda^{\alpha}\log\lambda + (\sigma_1^{\alpha}\log\sigma_1)\bar{F}}{(\alpha+1)\lambda^{\alpha} - \sigma_2\alpha\lambda^{\alpha-1}} \quad (9)$$

$$\frac{\partial\lambda}{\partial\bar{F}} = \frac{\sigma_1^{\alpha}}{(\alpha+1)\lambda^{\alpha} - \sigma_2\alpha\lambda^{\alpha-1}} \quad (10)$$

Factorial LTRE

A factorial (fixed factors: species and temperature) LTRE analysis was conducted following Caswell (2001). The whole parameter set was pooled for calculating the overall mean matrix ($\mathbf{A}\cdot\cdot$). Consequently:

$$\lambda^{(kl)} = \lambda^{(\cdot\cdot)} + \alpha^{(k)} + \beta^{(l)} + (\alpha\beta)^{(kl)} \quad (11)$$

where $\alpha^{(k)}$ and $\beta^{(l)}$ are the main effects of the k^{th} species and the l^{th} level of temperature, and $(\alpha\beta)^{(kl)}$ is the interaction effect. $\lambda^{(\cdot\cdot)}$ refers to the population growth rate of the overall mean matrix ($\mathbf{A}\cdot\cdot$). These effects were decomposed into contributions from each matrix element:

$$\alpha^{(k)} = \sum_i (p_i^{(k\cdot)} - p_i^{(\cdot\cdot)}) \left.\frac{\partial\lambda}{\partial p_i^{(k\cdot)}}\right|_{P/2} \quad (12)$$

$$\beta^{(l)} = \sum_i (p_i^{(\cdot l)} - p_i^{(\cdot\cdot)}) \left.\frac{\partial\lambda}{\partial p_i^{(\cdot l)}}\right|_{P/2} \quad (13)$$

$$(\alpha\beta)^{(kl)} = \sum_i (p_i^{(kl)} - p_i^{(\cdot\cdot)}) \left.\frac{\partial\lambda}{\partial p_i^{(kl)}}\right|_{P/2} - \alpha^{(k)} - \beta^{(l)} \quad (14)$$

One-way LTRE

For each species, the effect of each temperature level on λ is measured relative to 25°C, for which we obtained the reference matrix $\mathbf{A}^{(r)}$. The total temperature effect on λ is decomposed into contributions of the four defined vital rates to the observed difference of the λ-value of the treatment relative to the reference $\lambda^{(r)}$. Each contribution is composed by the observed change in the vital rate parameter owing to the temperature decrease, and the sensitivity of λ to changes in the parameter,

$$\lambda^{(k)} \approx \lambda^{(r)} + \sum_i \left(p_i^{(k)} - p_i^{(r)}\right) \left.\frac{\partial\lambda}{\partial p_i}\right|_{P/2} \quad (15)$$

where p_i are vital rate parameters at treatment k and reference r, and sensitivities are evaluated at the mean of both parameter sets ($P/2$).

We used a bootstrap resample procedure to calculate 95% confidence intervals for λ, σ_1, σ_2, α and $\bar{F}$ through the percentile method, with a resampling size of 5000 (Meyer *et al.* 1986; Manly 1997). In order to detect differences among population growth rates under different treatments, individuals and their life histories among treatments were permuted, according to Manly (1997), with 5000 randomizations. We calculated the statistic θ after each permutation, defined by Levin *et al.* (1996) as the difference in λ in the k treatment, relative to reference, that is,

$$\theta = \left|\lambda^k - \lambda^r\right| \quad (16)$$

If the observed value is outside 95% of the distribution of θ obtained by permutations, a significant difference between growth rates is accepted.

Body size data

Starting with a cohort of 10 newborn females of each species, we measured daily the cladoceran body length from the top of the head to the base of the caudal spine. This was done until death of all individuals, at 20 ± 1°C and a saturating food level. We defined the adult body size as the length of the individuals at the age of 23 days, where animals of all species reached a size statistically undistinguishable from that of later ages. The average adult body length for each species was converted to body mass using the standard length-weight regression of Bottrell *et al.* (1976) for cladocerans.

RESULTS

The distribution of field population densities of the study species over three temperature ranges is shown in Figure 2. ANOVA by ranks and post hoc tests results (Fig. 2) indicated that density of *D. chilense* was significantly higher at high temperature than medium temperature. Species *D. ambigua* had highest densities at low temperatures, whereas *C. dubia* did not show significant differences over the observed temperature range. Finally, *M. micrura* exhibited highest densities at high temperatures.

From the experimental results, we observed that population growth rate λ increased with temperature for all species (Fig. 3). The growth rate of *D. ambigua* reflects a small variation across the temperature range (19%), followed by *D. chilense* (36%) and *C. dubia* (42%). The strongest differences were found for *M. micrura* (300%).

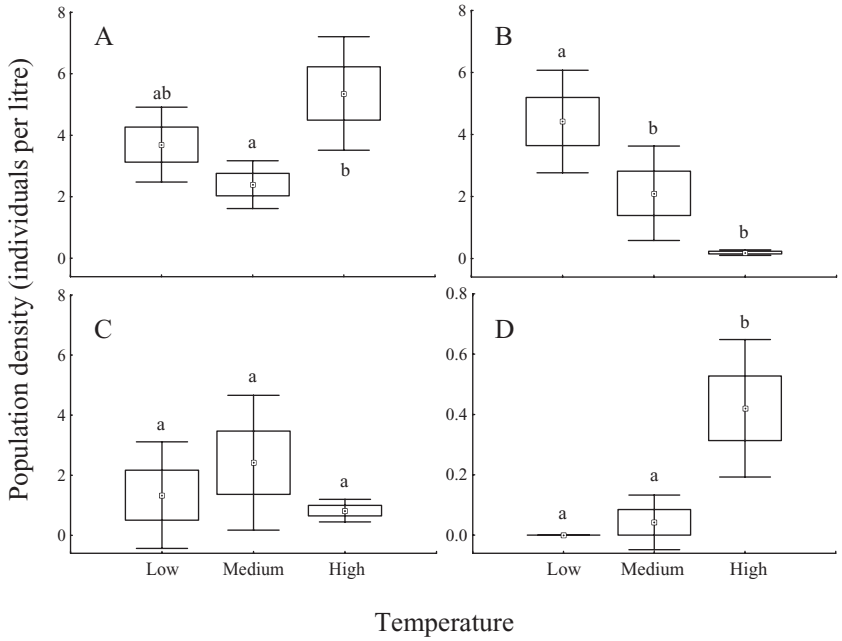

Fig. 2. Box plots (mean, standard error, 95% confidence interval) of field population densities of cladoceran species over field temperature. Temperature ranges are low (<12.5°C), medium (12.5–17.5°C) and high (>17.5°C). Significant differences at a 0.05 level (multiple comparisons by ranks) are shown. A: *Diaphanosoma chilense*, B: *Daphnia ambigua*, C: *Ceriodaphnia dubia* and D: *Moina micrura*.

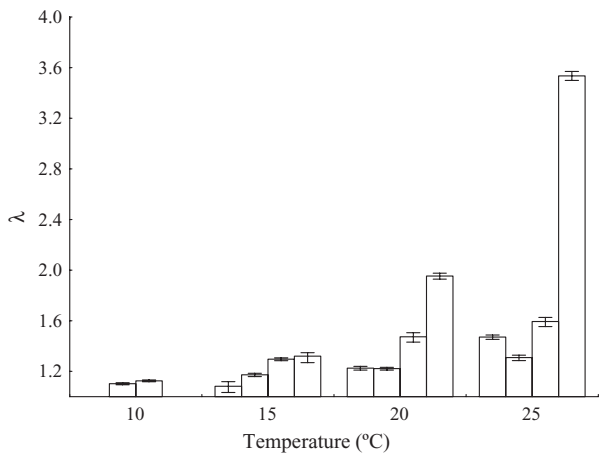

Fig. 3. Population growth rate estimates for four cladoceran species at temperatures of 10°C, 15°C, 20°C and 25°C. The bars within each temperature represent, respectively: *Diaphanosoma chilense* (except at 10°C), *Daphnia ambigua*, *Ceriodaphnia dubia* and *Moina micrura* (except at 10°C). Error bars correspond to 95% bootstrap confidence intervals. All differences were significant, both between temperatures for a given species and between species for a given temperature.

As *M. micrura* and *D. chilense* did not reproduce before dying at 10°C, we removed that temperature level in order to obtain a balanced design for the factorial analysis. Nonetheless, they were included in the one-way analyses. The factorial LTRE results indicated that the growth rate of *M. micrura* exhibited the largest (and positive) effect on variation of λ with respect to the overall mean, while *D. ambigua* exhibited the only negative effect, *D. chilense* showed a small positive effect, and *C. dubia* exhibited growth rates with values close to the overall mean (Fig. 4A). Figure 4B shows that increasing temperature always drove higher growth rates. Nevertheless, the pattern of temperature-driven variation of λ differed between species, as shown by the species-by-temperature effects (Fig. 5). Note that *M. micrura* exhibited the largest deviation in growth rates with respect to the additive model, and *D. chilense* showed negative contributions at the three observed temperatures. As temperature increased, the interaction effects decreased for *D. chilense*, *D. ambigua*, and *C. dubia*, but increased for *M. micrura*. At the highest tested temperature (25°C) *M. micrura* presented a large positive interaction effect, and all other species showed negative effects. Conversely, at 15°C *D. ambigua* showed the larger positive contribution, whereas *M. micrura* showed the most negative contribution.

The one-way LTRE results for *D. chilense* revealed that parameters σ_2, α and $\bar{F}$ contributed significantly and negatively to population growth rate (Fig. 6A). Decreasing temperatures led to a decrease in λ, mainly through a delay in age at maturity and secondarily by decreasing fecundity, while reduced adult survivorship had a minor impact. For *D. ambigua* the same

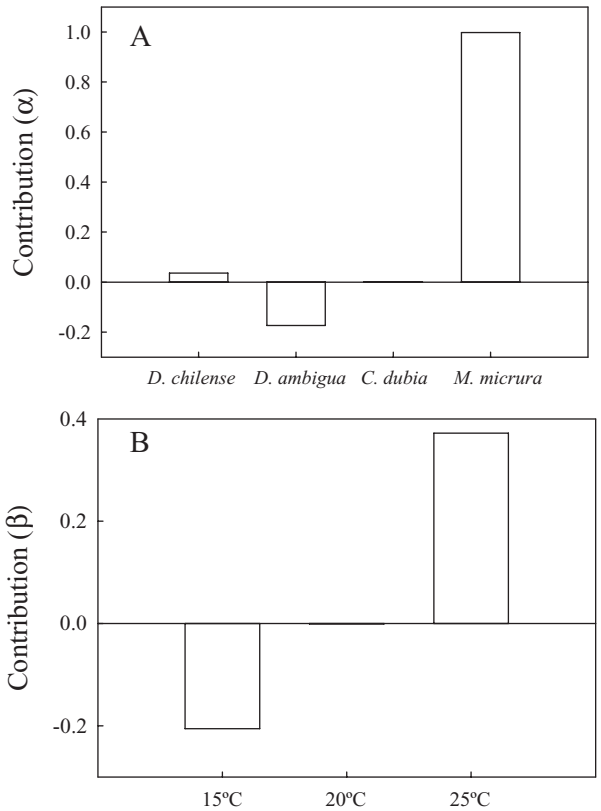

Fig. 4. Factorial life table response experiments contributions to population growth rate variation. A: main effects of species, B: main effects of temperature reduction.

parameters contributed significantly to population growth, with α and $\bar{F}$ contributing negatively and σ_2 positively. For this species, the strongest contribution was from age at maturity at 10 and 15°C and by $\bar{F}$ at 20°C. The contributions of σ_2 were clearly overwhelmed by the negative contributions of α and $\bar{F}$ (Fig. 6B). For *C. dubia*, negative contributions of age at maturity were stronger at lower temperatures. The contribution of $\bar{F}$ was significant and negative at every temperature except at 20°C, where the positive contribution of $\bar{F}$ was overwhelmed by the effect of α, resulting in a net λ decrease at 20°C relative to 25°C (Fig. 6C). For *M. micrura*, α and $\bar{F}$ contributed significantly to the decrease of λ as temperature was lowered. The contribution of $\bar{F}$ was more important at 20°C than at 15°C, but nonetheless the strongest contribution came from α, which was larger over the entire range. All the significant contributions were negative (Fig. 6D).

DISCUSSION

Although the importance of temperature for life history and demography of cladocerans is well established (see earlier references), most early experimental work focused on responses of single-species either to temperature only, or in combination with factors such as food (Giebelhausen & Lampert 2001), predation risk (Sakwinska 1998; Lass & Spaak 2003), or both (Weetman & Atkinson 2002). Moreover, the demographic mechanisms by which variables affect growth rates of target species are not well resolved in most studies, as for that purpose the observed change in a given life history trait needs to be weighted by the sensitivity of the growth rate to changes in that trait. In this work we made use of matrix population modelling and analysis with parameterization from a life table experiment arranged in a four-species by four-temperatures design, in order to assess the interspecific variation in the response of vital rates to temperature of a group of coexisting cladocerans.

Comparing patterns of body size and population abundance of western-hemisphere cladocerans across latitude, Gillooly and Dodson (2000) suggested that the seasonal dynamics of *Daphnia* is mainly governed by temperature change. Accordingly, in this study we report that the seasonal patterns of abundance of a cladoceran assemblage in the field are related to changes in temperature. In our study site, *D. chilense* and *M. micrura* populations peaked in density mainly at high temperature, *D. ambigua* at low temperature, and *C. dubia* did not show any specific trend. Therefore, regarding the first question posed in the introduction, our data suggested that seasonal trends of species abundance translate to differential trends of temperature exposure. Our LTRE analyses confirmed that the potential population growth rates varied among species and temperature, in agreement with the field patterns.

Our results confirmed that, within the tested range, temperature positively affected λ of all species under study (Figs 3,4B). The main effects of species (Fig. 4A) showed that *M. micrura* exhibited the highest potential for population growth, followed by *D. chilense* and *C. dubia*, whereas *D. ambigua* presented the lowest λ-values. Therefore, species with higher growth potential exhibited higher abundances during warmer seasons.

An analysis of the interaction effects (Fig. 5) revealed that *M. micrura* exhibited a higher growth rate than expected by the additive model under high temperature, and *D. ambigua* did the same under low temperature. Furthermore, *M. micrura* showed a large decrease in λ at 15°C relative to that expected by the additive model. Moreover, *M. micrura* and *D. chilense* were unable to reproduce in the lab under the minimal temperature (10°C). This supported the hypothesis that the cold-growing species (*D. ambigua*) is relatively favoured by low temperature, and the warm-growing species (*M. micrura*) is relatively favoured by high temperature. On the other hand, *C. dubia* growth rate behaved close to the additive model, whereas

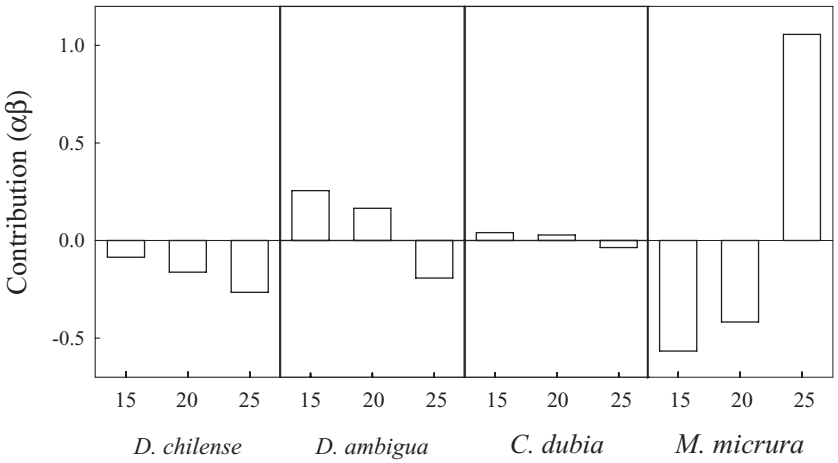

Fig. 5. Life table response experiments contributions of interaction effects (species–temperature).

D. chilense showed lower λ than expected if no interactions take place. Nonetheless, the negative interaction effects at 25°C were a consequence of the high contribution of that temperature level which resulted from the extreme λ of *M. micrura*.

Moina micrura showed the largest growth potential among the tested species, but this potential is likely never reached in Lake El Plateado. During summer, the predation risk is higher, and if predation accounts for the decreased realized λ of *M. micrura* in the field, this species could only persist with high birth rates, which can be attained under high temperature. This is the strategy (i.e. maximization of birth rate) attributed to *D. galeata* in Lake Constance (Stich & Lampert 1981). Although *D. chilense* also presents higher densities in the summer, this population exhibits diel vertical migration (Ramos-Jiliberto *et al.* 2004). Therefore, and assuming that these two species share predators and food, it seems likely that predation is limiting the abundance of *M. micrura* in this system.

In agreement with earlier works (Bottrell 1975a,b) our one-way LTRE results revealed that changes in age at first reproduction exerted the highest contribution to the observed changes in λ for all the species in response to temperature reduction (see Fig. 6). This means that, except for *D. ambigua* at 20°C, delayed maturation explains most of the λ decrease in all treatments. Nevertheless, fertility reduction at lower temperatures also exerted a significant contribution to variation in λ; and the magnitude of this effect was considerable in most treatments. The case of *C. dubia* represents a positive contribution of fertility at 20°C relative to control (Fig. 6), this means that increasing fecundity enhanced the growth rate in opposition to the observed delayed age at maturity, which decreased λ. The net result was a reduced λ at 20°C because the magnitude of the effect of α was larger than the magnitude of the opposite effect of fertility. Finally, adult survival exerted a small but significant effect on changes in λ in all temperature treatments of *D. chilense* (negative contributions) and *D. ambigua* (positive contributions, see Fig. 6). Regarding the last question posed in the introduction, our results indicated that the demographic mechanism of temperature-driven λ reduction is a combination of delayed age at maturity and fertility changes.

How do our measurements compare with theoretical expectations? The emerging metabolic theory of ecology (Brown *et al.* 2004) predicts that metabolism as well as higher-level population processes are mainly determined by body size and temperature (Gillooly *et al.* 2001, 2002). Specifically, intrinsic population growth rate (r_{max}) is expected to be related to body mass (M) and absolute temperature (T) as (Savage *et al.* 2004):

$$r_{max} \propto M^{-1/4} e^{-E/kT} \quad (17)$$

where E and k are the activation energy and Boltzmann's constant, respectively. Two main predictions arise from that theory: (i) there is a negative linear relationship between mass-corrected intrinsic growth rate (i.e. $\ln(r_{max} M^{1/4})$, with $r_{max} = (\ln\lambda)$ and the inverse of absolute temperature ($1/kT$); and (ii) the slope of that relationship gives the value of the activation energy E, which should fall within the range 0.2–1.2 (in eV units) expected for biochemical reactions (Gillooly *et al.* 2001). From our growth rate estimates and body size measurements of the same clones, we calculated the slope E for each of the studied species. All values of E were negative and between the expected values (with all $R^2 > 0.9$ and $P < 0.05$). The steepest slope was for *M. micrura* (–1.079), followed by *D. chilense* (–0.976), *C. dubia* (–0.658) and *D. ambigua* (–0.480). Steeper slopes were associated with larger intercepts. Therefore, after correcting for body size, the metabolic ecology model yielded the

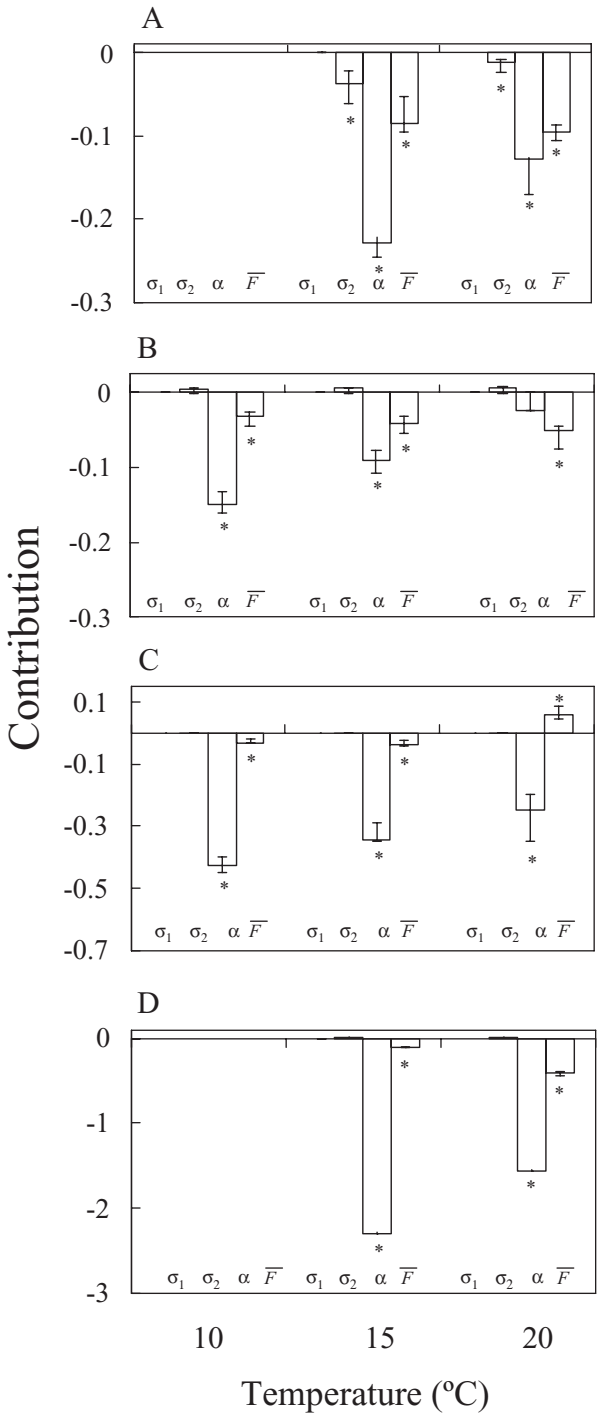

Fig. 6. Contribution of population parameters: juvenile survivorship (σ_1), adult survivorship (σ_2), age of maturity (α) and fertility ($\overline{F}$), to changes in the growth rate of *Diaphanosoma chilense* (A), *Daphnia ambigua* (B), *Ceriodaphnia dubia* (C), and *Moina micrura* (D), estimated by one-way life table response experiments for temperature reductions to 10°C, 15°C and 20°C relative to control (25°C). There are no measurements for A and D at 10°C. Bootstrap error bars correspond to 95% confidence intervals. Asterisk shows significant contributions.

same hierarchy of population growth potential as our demographic analyses. Even though our data included only a few species and temperatures, the LTRE analyses were in agreement with expectations arising from current theory, and provided a demographic explanation for the differences in species-specific patterns of temperature response in our system of study.

ACKNOWLEDGEMENTS

We thank the partial support from FONDECYT grant 1040821 and CONICYT-PBCT grant ACT34/2006 to RRJ and a CONICYT doctoral scholarship to AAA. The authors thank Francisco Hoecker-Escuti for his technical assistance in programming, and Michael Bull for final improvement of the manuscript.

REFERENCES

Berberovic R., Bikar K. & Geller W. (1990) Seasonal variability of the embryonic development time of three planktonic crustaceans: dependence on temperature, adult size, and egg weight. *Hydrobiologia* **203,** 127–36.

Bottrell H. H. (1975a) The relationship between temperature and duration of egg development in some epiphytic Cladocera and Copepoda from the River Thames, reading, with a discussion of temperature functions. *Oecologia* **18,** 63–84.

Bottrell H. H. (1975b) Generation time, length of life, instar duration and frequency of moulting, and their relationship to temperature in eight species of Cladocera from the River Thames, reading. *Oecologia* **19,** 129–40.

Bottrell H. H., Duncan A., Gliwicz Z. M. *et al.* (1976) A review of some problems in zooplankton production studies. *Nor. J. Zool.* **24,** 419–56.

Brown J. H., Gillooly J. F., West G. B. & Savage V. M. (2004) Toward a metabolic theory of ecology. *Ecology* **85,** 1771–89.

Burks R. L., Lodge D. M., Jeppesen E. & Lauridsen T. L. (2002) Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. *Freshwater Biol.* **47,** 343–65.

Burns C. W. (1969) Relation between filtering rate, temperature, and body size in four species of daphnia. *Limnol. Oceanogr.* **14,** 693–700.

Caswell H. (1996) Analysis of life table response experiments. II. Alternative parameterizations for size- and stage-structured models. *Ecol. Model.* **88,** 73–82.

Caswell H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*, 2nd edn. Sinauer Associates, Sunderland.

Cole P., Luecke C., Wurtsbaugh W. & Burkart G. (2002) Growth and survival of *Daphnia* in epilimnetic and metalimnetic water from oligotrophic lakes: the effects of food and temperature. *Freshwater Biol.* **47,** 1–10.

Dawidowicz P. & Loose C. J. (1992) Metabolic costs during predator-induced diel vertical migration of *Daphnia*. *Limnol. Oceanogr.* **37,** 1589–95.

De Meester L., Dawidowicz P., van Gool E. & Loose C. (1999) Ecology and Evolution of pedator-induced behavior and diel vertical migration. In: *The Ecology and Evolution of Inducible Defenses* (eds R. Tollrian & C. D. Harvell) pp. 160–76. Princeton University Press, Princeton.

Domínguez P., Zúñiga L. & Lembeye G. (1976) Condiciones químicas y físicas de la Laguna El Plateado, Chile. *Noticiero Mensual Museo Nacional de Historia Natural (Chile)* **29,** 3–11.

Domínguez P., Molina H. & Sáiz F. (1981) Variaciones temporales de las condiciones químicas de una laguna eutrófica de régimen monomíctico templado. *An. Mus. Hist. Nat. Valparaíso (Chile)* **14,** 175–84.

Geller W. (1987) On estimating the age and the development time of Daphnia as a function of body size and temperature. *J. Plankton Res.* **9,** 1225–30.

Giebelhausen B. & Lampert W. (2001) Temperature reaction norms of *Daphnia magna*: the effect of food concentration. *Freshwater Biol.* **46,** 281–9.

Gillooly J. F. & Dodson S. I. (2000) Latitudinal patterns in the size distribution and seasonal dynamics of new world, freshwater cladocerans. *Limnol. Oceanogr.* **45,** 22–30.

Gillooly J. F., Brown J. H., West G. B., Savage V. M. & Charnov E. L. (2001) Effects of size and temperature on metabolic rate. *Science* **293,** 2248–51.

Gillooly J. F., Charnov E. L., West G. B., Savage V. M. & Brown J. H. (2002) Effects of size and temperature on developmental time. *Nature* **417,** 70–3.

Goss L. B. & Bunting D. L. (1983) *Daphnia* development and reproduction: responses to temperature. *J. Therm. Biol.* **8,** 375–80.

Hall C. J. & Burns C. W. (2002) Mortality and growth responses of *Daphnia carinata* to increases in temperature and salinity. *Freshwater Biol.* **47,** 451–8.

Korpelainen H. (1986) Effects of temperature and photoperiod on life history parameters of *Daphnia magna* (Crustacea: Cladocera). *Freshwater Biol.* **16,** 615–20.

Lampert W. (1987) Predictability in lake ecosystems: the role of biotic interactions. *Ecol. Stud.* **61,** 333–46.

Lampert W. (1989) The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.* **3,** 21–7.

Lampert W. & Sommer U. (1997) *Limnoecology: The Ecology of Lakes and Streams*. Oxford University Press, New York.

Lass S. & Spaak P. (2003) Temperature effects on chemical signalling in a predator–prey system. *Freshwater Biol.* **48,** 669–77.

Lei C. H. & Armitage K. B. (1980) Growth, development and body size of field and laboratory populations of *Daphnia ambigua*. *Oikos* **35,** 31–48.

Lemke A. M. & Benke A. C. (2003) Growth and reproduction of three cladocerans species from a small wetland in the southeastern U.S.A. *Freshwater Biol.* **48,** 589–603.

Levin L., Caswell H., Bridges T., DiBacco C., Cabrera D. & Plaia G. (1996) Demographic responses of estuarine polychaetes to pollutants: life table response experiments. *Ecol. Appl.* **6,** 1295–313.

Loose C. & Dawidowicz P. (1994) Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. *Ecology* **78,** 2255–63.

McCauley E. (1984) The estimation of abundance and biomass of zooplankton in samples. In: *A Manual of Methods for the Assessment of Secondary Production in Fresh Waters* (eds J. A. Downing & F. H. Rigler) pp. 228–65. Blackwell Scientific Publications, Oxford.

Manly B. F. J. (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd edn. Chapman & Hall, London.

Meyer J. S., Ingersoll C. G., McDonald L. L. & Boyce M. S. (1986) Estimating uncertainty in population growth rates: Jacknife vs. Bootstrap techniques. *Ecology* **67,** 1156–66.

Ramos-Jiliberto R. & Zúñiga L. R. (2001) Depth-selection patterns and diel vertical migration of *Daphnia ambigua* (Crustacea: Cladocera) in lake El Plateado. *Rev. Chil. Hist. Nat.* **74,** 573–85.

Ramos-Jiliberto R., Flores F., Trapp C., Siebeck O. & Zúñiga L. R. (1997) Thermal, light and oxygen characteristics in a small eutrophic warm monomictic lake (El Plateado, Valparaíso, Chile). *Verh. Internat. Verein. Limnol.* **26,** 256–60.

Ramos-Jiliberto R., Trapp C., Flores F., Brignardello A., Siebeck O. & Zúñiga L. (1998) Seasonal succesion of planktonic crustaceans in a small eutrophic temperate lake (El Plateado, Valparaíso, Chile). *Verh. Internat. Verein. Limnol.* **26,** 1997–2000.

Ramos-Jiliberto R., Carvajal J. L., Carter M. & Zúñiga L. R. (2004) Diel vertical migration patterns of three zooplankton populations in a Chilean lake. *Rev. Chil. Hist. Nat.* **77,** 29–41.

Reichwaldt E. S. & Stibor H. (2005) The impact of diel vertical migration of Daphnia on phytoplankton dynamics. *Oecologia* **146,** 50–6.

Sakwinska O. (1998) Plasticity of *Daphnia magna* life history traits in response to temperature and information about a predator. *Freshwater Biol.* **39,** 681–7.

Savage V. M., Gillooly J. F., Brown J. H., West G. B. & Charnov E. L. (2004) Effects of Body Size and Temperature on Population Growth. *Am. Nat.* **163,** 429–41.

Siebeck H. O. (1980) Optical orientation of pelagic crustaceans and its consequence in the pelagic and littoral zone. In: *Evolution and Ecology of Zooplankton Communities* (ed. Kerfoot, W. C.) pp. 28–38. University Press of New England, Hanover.

Sommer U., Glimicz Z. M. & Lampert Duncan A. (1986) The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.* **106,** 433–71.

Stich H. B. & Lampert W. (1981) Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature* **293,** 396–8.

Vijverberg J. & Koelewijn H. P. (2004) Effect of temperature on development and growth of the raptorial cladoceran *Leptodora kindtii* under laboratory conditions. *Freshwater Biol.* **49,** 1415–22.

Weetman D. & Atkinson D. (2002) Antipredator reaction norms for life history traits in *Daphnia pulex*: dependence on temperature and food. *Oikos* **98,** 299–307.

Weetman D. & Atkinson D. (2004) Evaluation of alternative hypotheses to explain temperature-induced life history shifts in *Daphnia*. *J. Plank. Res.* **26,** 107–16.