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ECOSYSTEMS

Warming alters the metabolic rates and life-history parameters of *Ceriodaphnia silvestrii* (Cladocera)

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Abstract: Temperature rise has effects on the metabolic process of organisms, population structure, and ecosystem functioning. Here, we tested the effects of warming on the metabolic rates and life-history parameters of the widespread cladoceran *Ceriodaphnia silvestrii*. Two scenarios of global warming were established, an increase of 2 °C and an increase of 4 °C; the control temperature was 22°C. Our results showed that warming altered *C. silvestrii* metabolic rates, by increasing the rates of assimilation and secondary production, and decreasing the rates of filtration and ingestion. Warming also increased *C. silvestrii* fecundity and the body size of neonates and juveniles, and decreased the embryonic and post-embryonic time of development. *C. silvestrii* might be an important food resource at intermediary temperature as it had higher assimilation rates, even filtering fewer algae. At the highest temperature, we observed a substantial decrease in assimilation and secondary production, which could be a sign of stress starting. The increase in temperature by global warming will affect the cladocerans' metabolic processes and the population survival, even a small increase (2°C) might induce drastic fluctuations in such processes and affect the carbon and energy availability inside aquatic food-webs.

Key words: Ecosystem functioning, energy budget, freshwater ecosystem, zooplankton, global warming, population structure.

INTRODUCTION

The expected temperature increase in the forecasts for future climate scenarios (IPCC 2014) has concerned the scientific community in recent years, due to the strong effects of temperature on organisms, populations, and ecosystems (Yurista 1999, Jeppesen et al. 2010, Shurin et al. 2012, Šorf et al. 2015). Warming may lead to gradual losses of populations, reducing their growth and survival (Brown et al. 2004), by exceeding their tolerance limits (Loreau et al. 2001, Alcaraz et al. 2014). Or even, change species composition in natural environments, by favoring species with high thermal preferences and/or phenotypic plasticity (De-Meester et al. 2018).

In an organism level, temperature fluctuations affect the energy budget, which alters metabolic rates such as assimilation (Lampert 1977), filtration (Burns 1969, Geller 1975), respiration (Kobayashi 1974), and excretion rates (Yurista 1999, 2004). Such alterations affect the balance of energy distribution inside organisms, and consequently, alter their rates of growth and reproduction (secondary production, body size, fecundity, and development time). All these changes negatively affect the ecological interactions in which such organisms are involved and may also affect the population's

persistence in that thermal environment (Yurista 1999, Kooijman 2000). The metabolic rates mentioned affect the flow of energy and matter in aquatic ecosystems (Cabral & Marques 1999, Traill et al. 2010), as these processes are linked to energy contend of organisms (Gama-Flores et al. 2015), and energy transfer between trophic levels. Therefore, analyze the changes in life-history and the rates of secondary production, respiration, excretion, assimilation, and ingestion may help to better understand the response of populations to warming and evaluate the implications for ecosystem functioning (Sosnová & Klimešová 2009, Hébert et al. 2017).

In this context, subtropical freshwater environments are characterized by high biodiversity providing several ecosystem services, but it is predicted that these environments will be highly influenced by global warming due to the limited adaptations generated by the minor variations of the climate in the evolutionary time (Pörtner & Knust 2007). In these systems, among all communities, ectotherms such as zooplankton are more likely to be affected by this unpredictable warming, as these animals are not able to regulate their body temperature actively (Verberk et al. 2016). Each zooplanktonic species has its thermal history (thermal preference, phenotypic plasticity, and genetic responses) and will respond differently to changes in temperature (Loreau et al. 2001, De-Meester et al. 2018). For some species, a small increase of 2 °C leads to significant declines in growth, reproduction, and ingestion rates or can lead to the populations' extinctions due to high metabolic demands, as observed for *Daphnia magna* Straus, 1820 (Kooijman et al. 1989, Kooijman 2000). Such shifts alter the ecosystem functioning, as the changes in cladocerans' biomass alter also the structure of their prey and predators (O'Connor et al. 2009, Abo-Taleb 2019), and modify the nutrient's availability (Saba et al. 2009).

Subtropical freshwater environments have the predominance of small-bodied zooplankton, among them the cladocerans of the genus *Ceriodaphnia*, which present high abundances in these environments (Choueri et al. 2007, Lansac-Tôha et al. 2009, Brito et al. 2013, 2016). The filtration, assimilation, and excretion rates of these cladocerans directly affect the cycles of carbon and organic matter in subtropical aquatic environments (Hébert et al. 2017). Thus, studies on energy budget components, taking into account forecasted climate change (IPCC 2014), can highlight how warming affects the flux of energy and matter in freshwater ecosystems. Also, the use of native zooplankton species might show a more realistic response of the natural environments - and as far as we know, this is the first study investigating the metabolic rates of the cladoceran *C. silvestrii* regarding global warming scenarios.

Here, we analyze the effects of warming on the metabolic rates and life-history parameters of the cladoceran *Ceriodaphnia silvestrii* Daday, 1902. For that, we tested two scenarios, an increase of 2 °C and an increase of 4 °C in temperature. These scenarios represent, respectively, the optimistic and pessimistic forecasts of future global temperatures, according to the Intergovernmental Panel on Climate Change (IPCC 2014). As warming increases metabolic demands, we predict that with the increase of 2°C in the temperature *C. silvestrii* would present I) higher consumption rates (filtration and ingestion), higher respiration rates, higher assimilation rates, higher investment in secondary production (faster population growth through fecundity and time of development), and higher metabolic losses (excretion); and the increase of 4°C in the temperature would result in II) lower rates of filtration, ingestion,

secondary production, and assimilation, but we expect the highest metabolic losses (excretion) and respiration rates due to temperature stress.

MATERIALS AND METHODS

Alga and cladoceran stock cultures

Cells of *Raphidocelis subcapitata* (Korshikov) F. Hindák 1990 were obtained from cultures maintained at the Plankton Laboratory of the Federal University of São Carlos (SP, Brazil), where all the experiments were conducted. The Chlorophyceae *R. subcapitata* was weekly cultivated in Erlenmeyer flasks of 2 L filled with 1 L of CHU-12 as medium (Müller 1972). The algae were initially inoculated at 1 x 10^5 cells mL^{-1} and maintained at 25 ± 2 °C, under a 12:12 h (light/dark) photoperiod until reaching the stage of exponential growth. After that, the algal cultures were centrifuged to remove the CHU-12 medium (which can eventually become toxic to the zooplankton) and were subsequently stored at 4°C for up to one week, and this procedure was repeated until the end of the experiments.

Populations of *C. silvestrii* were sampled from different regions of two subtropical shallow lakes with similar characteristics (area of approximately 800 m^2 and 2.0 m of depth each one), localized around the city of São Carlos/São Paulo/Brazil. The individuals of *C. silvestrii* were acclimated and cultured for many generations (parthenogenetic reproduction), during approximately three months, in incubator chambers under controlled conditions of temperature (22°C = control, +2°C, and +4 °C) and photoperiod (12:12 h light: dark cycle). *C. silvestrii* were kept in 2 L beakers filled with 1.5 L of reconstituted water as the culture medium, with 50 adults per liter. This culture medium (reconstituted water) was prepared in the laboratory in agreement with standards described by the ABNT (2017), which include hardness from 40-48 mg $CaCO_3$ L^{-1}, pH from 7.0-7.6, and conductivity around 160 µS cm^{-1}. The culture medium was completely renewed three times a week, with new food added every time, which consisted of 1 x 10^5 cells mL^{-1} of *R. subcapitata* and a food supplement made from fermented fish food and yeasts (ABNT 2017).

Metabolic rates and secondary production experiment

To evaluate the effects of warming on metabolic rates and secondary production of *C. silvestrii* we first set up three temperatures (22°C = control, +2, and +4°C), including three replicates per temperature. In this first stage, 20 synchronized ovate females were put in each replicate (beaker) (based on previous experiments). To calculate biomass, we counted the number of eggs of each female and measured their body size (before the experiment started), corresponding to the distance between the superior extremity of the head and the end of the carapace (Hardy 1989). The experimental medium was completely renewed twice a week, by filtering the old medium with cladocerans in a net with mesh openings of 45 µm. The retained *C. silvestrii* were carefully transferred to the new medium, where pH, temperature, and food concentration was previously adjusted. The cladocerans were fed every two days during the experiment. The experiment was set up in incubator chambers under controlled conditions of temperature (cited above) and photoperiod (12:12 h light: dark cycle). *C. silvestrii* was kept in 2 L beakers filled with 1 L of reconstituted water as the experimental medium, the experiment was run for 15 days. The experimental period of 15 days was selected based on the life cycle of cladocerans (Allan 1976); this time is sufficient to analyze the zooplankton population's responses to the different treatments.

After 15 days we started the second stage: the filtration and ingestion experiment, which was conducted at the three temperatures (control, +2°C and +4°C), with three replicates per temperature. All individuals contained inside the beakers were placed into other 2 L beakers with 1 L of reconstituted water and 1 x 10^5 cells mL^{-1} of *R. subcapitata* (alga/food); three subsamples of each replicate were taken at 0 and 2 h to quantify the initial and final algal concentrations. Moreover, a control (no animals added) was incubated under the same experimental conditions, to evaluate only the algal growth after 2 h. All subsamples were fixed with 1% formaldehyde buffered with sodium borate, frozen in liquid nitrogen, and stored (-20 °C) until analysis. Defrosted samples (500 µL) were analyzed in a FACSCalibur cytometer (Becton and Dickinson Franklin Lakes, NJ, U.S.A.) equipped with a 15 mW Argon-ion laser (488 nm emission) using the FL3-H (red fluorescence) and the SSC-H (lateral dispersion) channels, following Sarmento et al.'s (2008) procedures. Fluorescent beads (6 µm, Fluoresbrite® carboxylate microspheres, Polysciences Inc., Warrington, PA, U.S.A.) were added to the samples, as an internal standard. The cytometry data were analyzed using FlowJo software, version 10.0 (Treestar.com, USA)."

With these data, we calculated the filtration rates (F) (µL *Ceriodaphnia*$^{-1}$ h^{-1}) and ingestion rates (I) (cells *Ceriodaphnia*$^{-1}$ h^{-1}). Filtration refers to the particles of the water that are filtrated by the cladocerans; while, the particles (i.e. the algae) that are taken to the cladoceran's mouth and digestive system for subsequent ingestion refers to ingestion (Bownik 2020). These rates were calculated according to the modified equation of Gauld (1951), with a correction factor (*A*):

$$F = \frac{V}{n} * \left[\frac{(lnC0 - lnCt)}{t} - A\right]$$

$$A = lnC0 - \frac{lnC't}{t}$$

$$I = F.\sqrt{C0}.Ct$$

where *C0* and *Ct* are, respectively, the initial and final algal concentration (cells mL^{-1}), *t* is the experimental time (hours) and *n* is the number of individuals in the volume *V* (mL). *A* refers to a correction factor for changes in the control with algal final concentration *C't* after the time *t*. The expression $\sqrt{C0}.Ct$ represents the geometric mean of food concentration (algal cells) during the time *t*.

In the third stage to estimate the respiration rates, also at the 15th day, we removed 18 *C. silvestrii* adults from each temperature (three replicates* six individuals * three temperature = 54 individuals) and placed in respirometric chambers (2 mL) containing sterile reconstituted water, at control, +2°C and +4°C. The decrease in the oxygen concentration was recorded for approximately 30 minutes using the Unisense micro-respiration system (Arhus, Denmark). The sensor signal was previously calibrated at 24 °C (mean of all treatments) using sterile and aerated water (100% of O_2 saturation) and a solution of 10 g/L sodium sulfite (0% O_2 saturation). Oxygen consumption rates R (µmol O_2 ind^{-1} h^{-1}) were calculated according to the equation described by Massarin et al. (2010):

$$R = [O_2]0 \times \frac{\left(1 - exp^{-kx\Delta t}\right)xV}{\Delta t}$$

where $[O_2]0$ was the oxygen concentration (µmol L^{-1}) measured at t = 0, V = the volume (L) of the respiration chamber, Δt = the incubation time, and *k* = the consumption coefficient (h^{-1}) obtained for the exponential models suitable for the oxygen concentration observed: $[O_2]_t = [O_2]0 \times exp^{-k \times t}$.

Finally, to estimate the secondary production after 15 days, the cladocerans were fixed in 4% formaldehyde buffered with borate and glucose, for better conservation and subsequent quantification. In fixed samples, we counted the number of individuals (*Ceriodaphnia* L^{-1}) for each size class (neonates, juvenile, adults, and ovate females) and the number of eggs inside each female' brood chamber. We calculated the dry weight (over 48 h/70°C) for each stage of development (five replicates - neonates, juvenile, adults, and ovate adults). We applied the length and weight measures in a regression formula (LnW = Ln*a* + *b* LnL) to calculate the biomass. The equation includes the weight logarithmic transformation (W) of dry weight µg (DW) and the length (L in mm), and *a* = intercept estimation and *b* = slope estimation. The secondary production (DW L^{-1} day^{-1}) was calculated according to Winberg et al.'s (1965) equation:

$$P = [(NI \times \Delta WI)\ TI^{-1}] + [(NII \times \Delta WII)\ TII^{-1}] + [(NIII \times \Delta WIII)\ TIII^{-1}]$$

where: I = neonates; II = juvenile; III = adults; NI, NII, and NIII are density data (*Ceriodaphnia* L^{-1}); ΔWI = (juvenile mean dry weight) - (neonate mean dry weight); ΔWII = (adult mean dry weight) - (juvenile mean dry weight); ΔWIII = (egg mean dry weight x mean of the number of eggs per female); TI = embryonic development time, TII = development time from neonate to juvenile, TIII = development time from juvenile to adult.

The assimilation and excretion rates were calculated from the modified equation of Petrusewicz (1967): Assimilation = Production + Respiration; and, Excretion = Ingestion - Assimilation

Life-history experiment

The experiment to study the life history parameters of *C. silvestrii* was conducted at the three temperatures (control, +2°C and +4°C) and photoperiod (12:12 h light: dark cycle). For this, neonates (< 24h old) were placed in 50 ml beakers (10 replicates per temperature, totalizing 30 replicates, with one neonate each) filled with reconstituted water as the experimental medium and 1×10^5 cells mL^{-1} of *R. subcapitata* (as food), the experimental medium and food were renewed every day. The bionomic parameters such as body length for all life stages (neonates, juveniles, and adults), the presence of exuviae (cladocerans' exoskeleton remaining from molt), egg-laying, and the number of eggs were daily observed in a stereomicroscope (Leica MZ6, Germany) until the third clutch (reproduction by parthenogenesis). From these observations were obtained the embryonic development time (EDT - the time from egg-laying to hatching), post-embryonic development time (PDT I - neonate to juvenile, PDT II - juvenile to adult, and primiparous- from neonate to the first clutch) (Kotov & Boikova 1998, Güntzel et al. 2003), and the body size mean of each development stage. The individuals of *C. silvestrii* were considered as neonates from birth until the first exuviae (cladocerans' exoskeleton remaining from molt); they were considered as juveniles from the first exuviae until before the first egg production; at the moment that they produced eggs for the first time they were considered as adults, and all these characteristics were observed daily under a stereomicroscope (Leica MZ6, Germany).

Statistical analysis

To evaluate the effect of warming on *C. silvestrii* metabolic rates, we performed a multivariate analysis of variance (MANOVA, to avoid type I error) (Gotelli & Ellison 2004), followed by analyses of variance (ANOVAs) and post-hoc Tukey analyses. For the mentioned analyses, temperature (control, +2 °C and +4 °C) was used as the categorical predictor variable, and

the rates of filtration, ingestion, secondary production, respiration, assimilation, and excretion were used as response variables. Regarding the secondary production rates in the analyses of variance, the difference between the final and initial experimental values was considered. The response variables were log-transformed to achieve the assumption of normality. The significance of MANOVA was reported using Pillai's trace, and the p-values. All the assumptions were tested and, the significance level adopted was $p \leq 0.05$. Analyses of variance (ANOVAs) applying *Bonferroni correction* (0.05/6 = 0.008, adjusted p-values for multiple comparisons; Gotelli & Ellison 2004) were performed to verify which response variables differed between treatments, and post-hoc Tukey analyses were used to verify which treatments differed from each other.

Due to the absence of normality assumption, Kruskal-Wallis tests were performed to analyze the effect of warming (control, +2 °C and +4 °C - categorical predictor variable) on the body-size of the development stages (neonate, juvenile and adult), fecundity, and development time stages (embryonic development time - EDT; post-embryonic age - PDT I and PDT II; primiparous age). Post-hoc analyses (Wilcoxon test) were performed to analyze at which temperatures these response variables differ. All analyses were performed using the package "stats" in R (R Core team 2019).

RESULTS

Metabolic rates

Warming affected the metabolic rates of *C. silvestrii* (MANOVA: F = 28.828, p = 0.002), altering the rates of secondary productivity (ANOVA: F = 11.76, p = 0.007), assimilation (ANOVA: F = 16.62, p = 0.003), filtration (ANOVA: F = 38.19, p < 0.001), and ingestion (ANOVA: F = 22.25, p = 0.001) (Figure 1). We observed a tendency of progressive decreases in respiration, and excretion with temperature rise, but these rates did not differ significantly (Table I). Concerning secondary productivity, the control temperature presented the lowest values (approx. 20 µg DW L^{-1} Day^{-1}), and +2°C the highest (approx. 140 µg DW L^{-1} Day^{-1}) (Figure 1a). Filtration and ingestion rates presented the highest values at the control temperature (approx. 550 µL *Ceriodaphnia*$^{-1}$ h^{-1}, and x10^4 cells *Ceriodaphnia*$^{-1}$ h^{-1}, respectively), decreasing at +2°C and +4°C (Figure 1b, c). We observed the highest values of assimilation rates (approx. 6.5 µg *Ceriodaphnia*$^{-1}$ h^{-1}) at +2°C, followed by +4°C and control (Figure 1d).

Life-history parameters of *C. Silvestrii*

C. silvestrii fecundity was significantly different among the temperatures (Kruskal-Wallis: Chi-square= 7.581, p = 0.022), the highest value was observed at +2°C (approx. 2 eggs/female), followed by +4°C and control (Figure 2). The body-sizes of *C. silvestrii* neonates (Kruskal-Wallis: Chi-square: 17.642, p = 0.000) and juveniles (Kruskal-Wallis: Chi-square: 11.626, p = 0.003) were also affected by warming, the highest values for both stages were observed at +2°C (approx. 0.4 and 0.55 mm, respectively) (Figure 3). Adult body size did not differ significantly among temperatures (p = 0.907) (Figure 3).

Warming had an effect on all development stages: embryonic (Kruskal-Wallis: Chi-square: 10.498, p = 0.005), primiparous age (Kruskal-Wallis: Chi-square: 23.022, p < 0.001), post-embryonic development time I (Kruskal-Wallis: Chi-square: 5.994, p = 0.049), and post-embryonic development time II (Kruskal-Wallis: Chi-square: 23.053, p < 0.001) (Figure 4). Embryonic and post-embryonic development time I (PDT I - neonate to juvenile) decreased progressively with the temperature increase. Whereas primiparous and post-embryonic development time II (juvenile

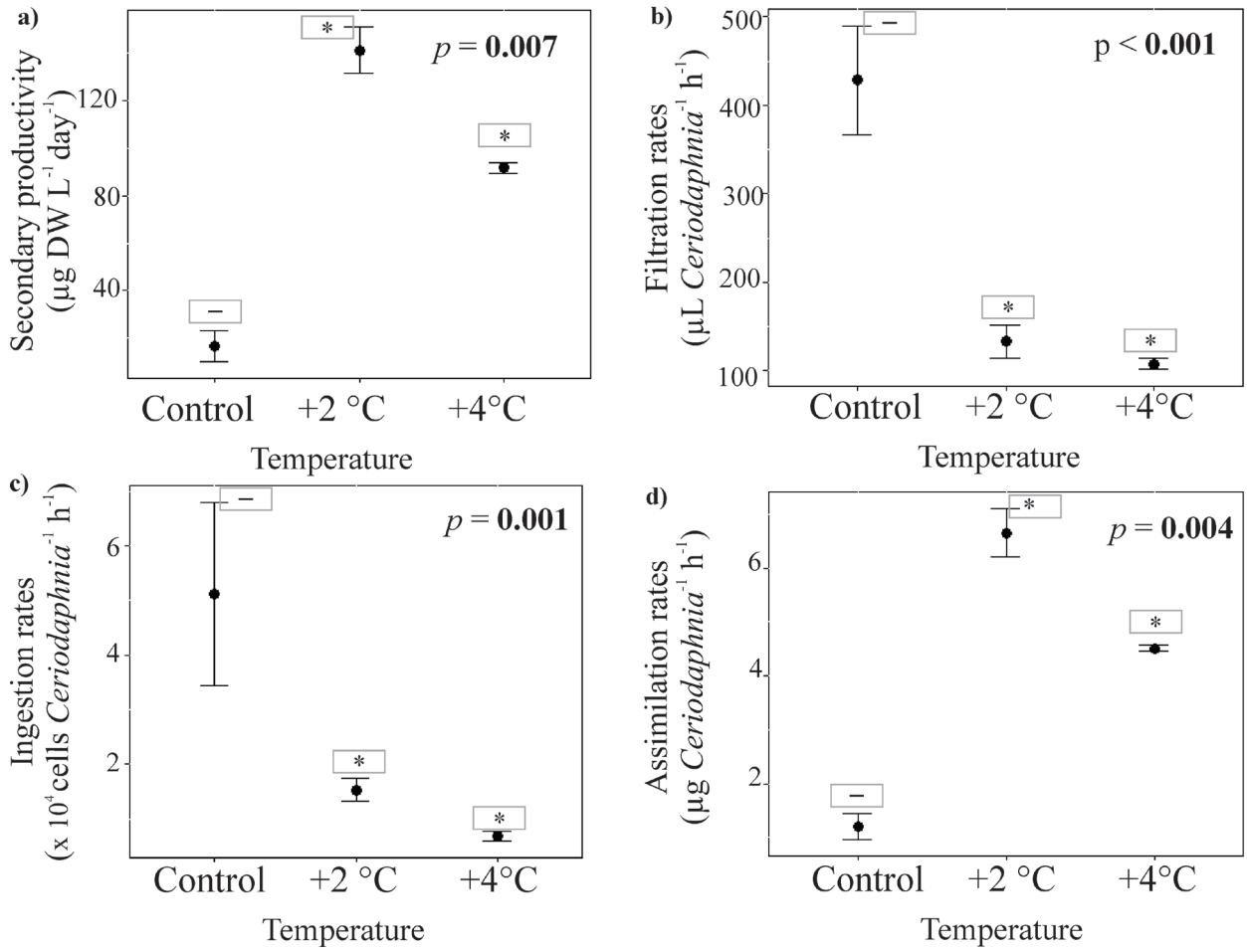

Figure 1. Box plot showing *C. silvestrii* metabolic rates, a) Secondary productivity, b) Filtration rates, c) Ingestion rates and d) Assimilation rates at three temperatures (control, +2 and +4°C), p-value from ANOVA analyses is shown. Symbols(-,*) above the columns indicate significant differences in post-hoc analyses - treatments that share a symbol do not differ significantly, p>0.05. • indicates the mean, ± standard error bars are shown.

to adult) had the highest values at the control and lowest at +2°C (Figure 4).

DISCUSSION

Warming has effects on several ecological process and organization levels, here we observed that the small-bodied cladoceran *C. silvestrii* decreased progressively its filtration and ingestion rates with the increase in temperature, while increased the assimilation and secondary production with slight warming and decreased again at the highest temperature. Warming also increased *C. silvestrii* neonates and juveniles body size, and adults' fecundity; and accelerated the time of development. An unbalance of energy production and transfer is reveal by the alteration of metabolic rates and life-history parameters analyzed - due to warming. These alterations affect food-web dynamics in freshwater ecosystems (O'Connor et al. 2009, Gama-Flores et al. 2015, Hébert et al. 2017, Abo-Taleb 2019).

Different than expected, *C. silvestrii* reduced progressively its filtration and respiration rates with warming from 22°C to 26°C. Some Daphiniidae species such as *Daphnia magna*, *D. galeata*, *D. ambigua*, and *D. pulicaria*

Table I. Initial and final average of *C. silvestrii* population rates, respiration, and excretion rates in the different temperatures. Note: ind. = individual. DW = dry weight. SE = standard error and SD = standard deviation. *Non-significant results.

Rates and attributes	Control	+2°C	+4°C	ANOVA*
Initial density (ind. L^{-1})	20.0	20.0	20.0	
Initial biomass (µg DW)	45.57	46.04	45.43	
Initial secondary productivity (µg DW L^{-1} day^{-1})	11.13	16.84	16.20	
Final density (ind. L^{-1})	305.66	1044.09	520.18	
Final biomass (µg DW)	447.45	2215.98	1103.72	
Respiration (µmol O_2 *Ceriodaphnia*$^{-1}$ h^{-1})	Mean = .054 SE ± .016 SD ± .029	Mean = .039 SE ± .004 SD ± .007	Mean= .016 SE ± .006 SD ± .01	F = 4.905 p = 0.06
Excretion (x 10^4 µg *Ceriodaphnia*$^{-1}$ h^{-1})	Mean = 4.31 SE ± 2.19 SD ± 3.80	Mean = 1.52 SE ± 0.21 SD ± 0.37	Mean = 0.68 SE ± 0.08 SD ± 0.15	F = 4.309 p = 0.07

present their grazing effectiveness around 25°C (Burns 1969, West & Post 2016), whereas *D. schodleri* and *D. pulex* at lower temperatures as 20°C (Burns 1969). Cladoceran species may also present contrasting responses in the relationship warming-respiration rates (Duval & Geen 1976, Goss & Bunting 1980, Forster et al. 2011a, Gerke et al. 2011). The different responses among species are possibly related to their geographical distribution and phenotypic plasticity (Gerke et al. 2011, De-Meester et al. 2018). Every species has a thermal window where their molecular, cellular, and systemic processes are optimized (Pörtner & Farrell 2008). Thus, high temperatures are linked to high metabolic demands, which might decrease: the carrying capacity of the zooplankton species (Allen et al. 2002), the rates of attack and manipulation on preys (Dell et al. 2014, West & Post 2016), and the predation effectiveness (i.e. filtration). Slight warming as 2 °C is sufficient to induce such decreases, as observed for *D. magna* by Kooijman et al. (1989), in agreement with our finds. Also, at high temperatures the organism's demand for oxygen increase in the same way that oxygen turns rarefied, limiting the species reaction and survival in aquatic environments (Verberk et al. 2016).

As we observed, the organisms' metabolic processes respond to warming in a correlated way due to the metabolic demands, i.e. higher respiration rates are linked to higher filtration rates (Kooijman 2000). Also, warming might lead to incomplete digestion by reducing the time that the nutrient remains inside the body (Kooijman 2000), reflecting in higher excretion values and lower assimilation. Although *C. silvestrii* had ingested the highest number of algal cells at the lowest temperature it also had the highest metabolic losses at this temperature (higher excretion and respiration and lower assimilation), and smaller-bodied neonates and

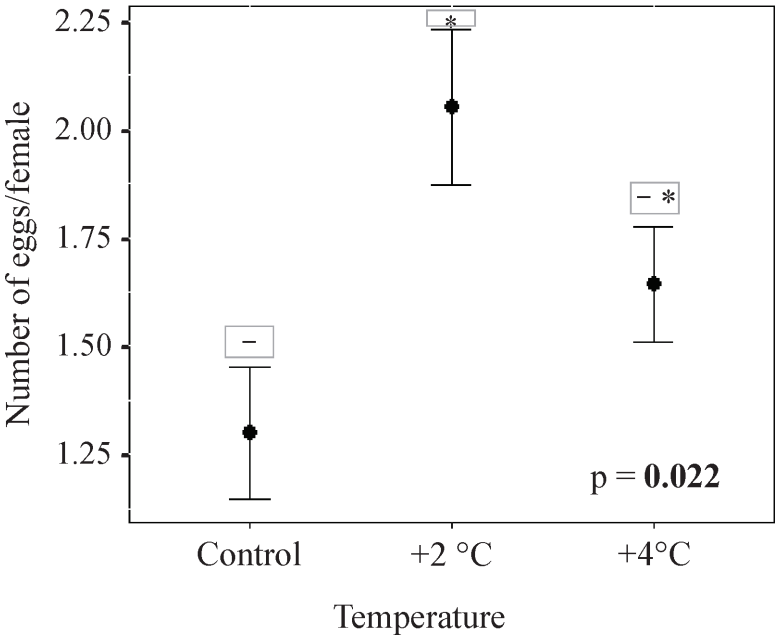

Figure 2. Box plot showing *C. silvestrii* fecundity (average of the number of eggs/ female from the three clutches) at three temperatures (control, +2, and +4°C), Kruskal-Wallis significant analyses (p = 0.022) are shown. Symbols (-,*) above the columns indicate significant differences (post-hoc analyses) - treatments that share a symbol do not differ significantly, p >0.05. • indicates the mean, ± standard error bars are shown.

juveniles. The opposite occurred at +2°C, where *C. silvestrii* presented larger-bodied neonates and juveniles and higher assimilation rates.

Other factors as age-depending responses and availability of high-quality fatty acids at high temperatures might also play a role in *C. silvestrii* responses. The quantity and quality of lipids reserves affect the growth and reproduction of cladocerans species, and it is related to temperature variations (Brett et al. 2006, Masclaux et al. 2012). Gama-Flores et al. (2015) observed crescent percentages of fatty acids in adult *Moina macrocopa* with warming up to 25°C, in contrast, in this same study neonates contained much higher proportions of these reserves, regardless of temperature regimes. These energy reserves in neonates promote reproductive maturity and offspring production, and in all stages might allow adaptation in natural populations to climate variation (Masclaux et al. 2012, Gama-Flores et al. 2015). Cladocerans fatty acids are assimilated from food - algae -, which in turn adjust them in their cellular membranes at high temperatures: producing more saturated fatty acids (Gladyshev et al. 2014). So, the high secondary production, assimilation, and fecundity of *C. silvestrii* at +2°C might represent an indirect effect of algae quality-contend *versus* temperature, through the filtration process.

We observed that at +2°C, *C. silvestrii* presented the fastest maturation, greatest fecundity, largest neonates and juveniles body-size, and greatest secondary productivity, contrasting the temperature size rule - which predicts that ectotherms grow fast at high temperatures and present smaller body sizes (biomass) (Atkinson 1994, Forster et al. 2011b, Hoefnagel et al. 2018). Furthermore, these responses observed for *C. silvestrii* represent tradeoffs between temperature changes and estimators of energetic gains and losses, showing efficiency in converting food into biomass at intermediate temperature. At the lowest and highest temperature, *C. silvestrii* reduced fecundity, neonates, and juveniles body-size, and delay maturation because at these same temperatures this species also presented high metabolic losses, and possibly had lower lipids reserves. Even though there was not a significant

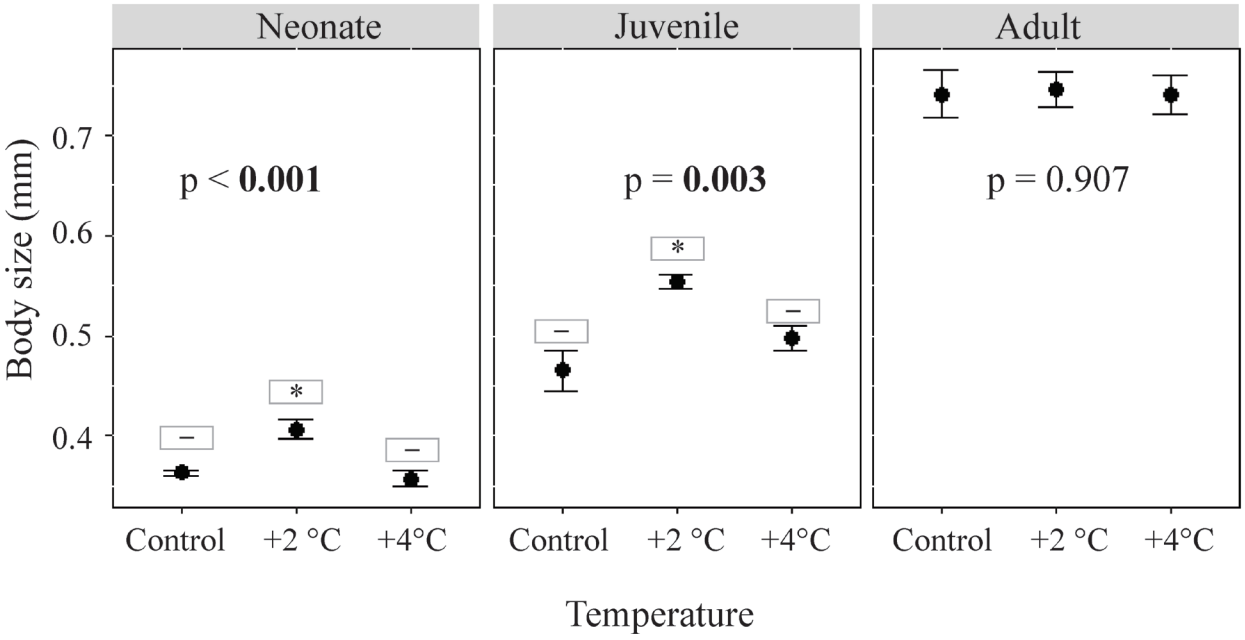

Figure 3. Box plot showing *C. silvestrii* body size (mm) in different development stages: neonate, juvenile, and adult (average from the three clutches) at three temperatures (control, +2, and +4°C), p-value from Kruskal-Wallis analyses are shown. Symbols(-,*) above the columns indicate significant differences in post-hoc analyses - treatments that share a symbol do not differ significantly, p >0.05. • indicates the mean, ± standard error bars are shown.

difference between secondary production at +2°C and +4°C, we observed lower values at the highest temperature, which might indicate that if the temperature continued to increase, this rate could decay even further, because of physiological stress (Savage et al. 2004).

Finally, the alteration of metabolic rates of *C. silvestrii* by warming has ecological implications on aquatic food-webs dynamics. The highest assimilation values, even consuming a lower number of algal cells, turn this species a food resource with high energy content for small-bodied fishes, natural predators of *C. silvestrii* in subtropical systems (Lazzaro 1987), and increase the amount of energy transferred to higher levels (Lang et al. 2017). Also, warming might at the same time: reduce the cladocerans density, and increase algal growth - prevailing non-edible algae (Visser et al. 2016). This could alter the trophic status of freshwater environments, causing unpleasant consequences for water quality and human well-being (Brooks et al. 2016).

CONCLUSIONS

Besides *C. silvestrii* is a subtropical species, it has a short thermal window, with thermal preferences around 24°C (i.e. greater food assimilation and biomass production). The increase in temperature by global warming (IPCC scenarios tested) will affect the cladocerans metabolic processes and the population survival, even a small increase (2°C) might induce drastic fluctuations in such processes and affect the carbon and energy availability inside aquatic food-webs, altering the entire ecosystem functioning.

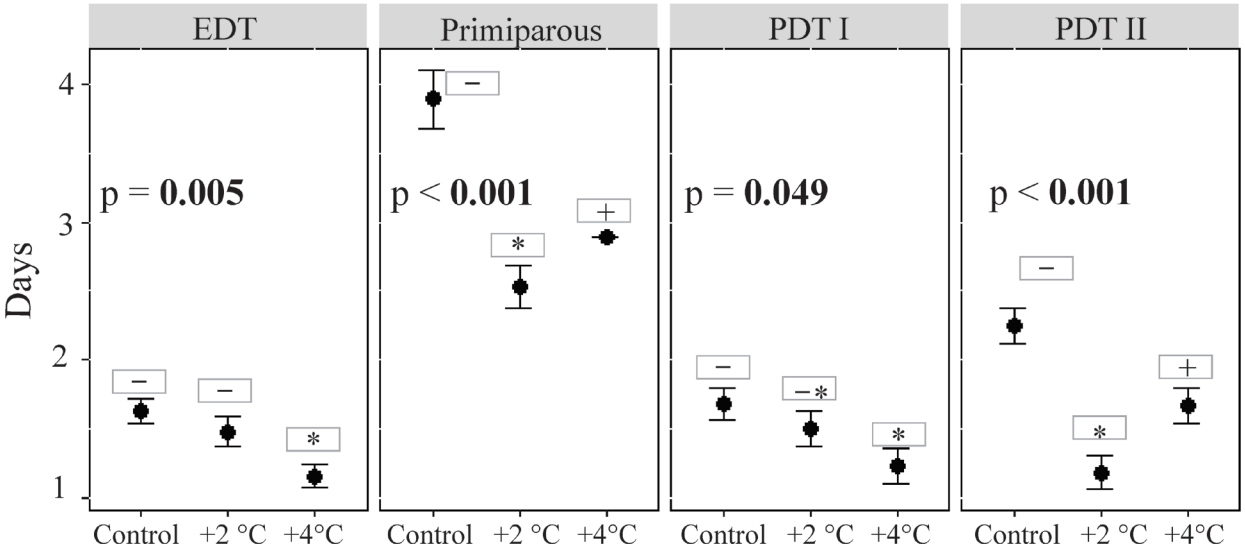

Figure 4. Box plot showing *C. silvestrii* development time in days (EDT = embryonic development time; Primiparous = from neonate to the first clutch; PDT I = neonate to juvenile; PDT II = juvenile to adult) at three temperatures (control, +2 and +4°C), p-value from Kruskal-Wallis analyses is shown. Symbols (-,*,+) above the columns indicate significant differences in post-hoc analyses - treatments that share a symbol do not differ significantly, p >0.05. • indicates the mean, ± standard error bars are shown.

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REFERENCES

ABNT- ASSOCIAÇÃO BRASILEIRA DE NORMAS TÉCNICAS. 2017. Aquatic ecotoxicology — Chronic toxicity — Test method with *Ceriodaphnia* spp. (Crustacea, Cladocera). Brazil.

ABO-TALEB H. 2019. Importance of Plankton to Fish Community. In: Biological Research in Aquatic Science. London, United Kingdom: IntechOpen Limited, p. 1-10.

ALCARAZ M, FELIPE J, GROTE U, ARASHKEVICH E & NIKISHINA A. 2014. Life in a warming ocean: Thermal thresholds and metabolic balance of arctic zooplankton. J Plankton Res 36: 3-10.

ALLAN JD. 1976. Life History Patterns in Zooplankton. Am Nat 110: 165-180.

ALLEN AP, BROWN JH & GILLOOLY JF. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science 297(80): 1545-1548.

ATKINSON D. 1994. Temperature and Organism Size-A Law for Ectotherms? Adv Ecol 25: 1-58.

BOWNIK A. 2020. Physiological endpoints in daphnid acute toxicity tests. Sci Total Environ 700: 134400.

BRETT MT, MULLER-NAVARRA DC, BALLANTYNE AP, RAVET JL & GOLDMAN CR. 2006. Daphnia fatty acid composition reflects that of their diet. Limnol Oceanogr 51: 2428-2437.

BRITO SL, MAIA-BARBOSA PM & PINTO-COELHO RM. 2013. Length-weight relationships and biomass of the main microcrustacean species of two large tropical reservoirs in Brazil. Brazilian J Biol 73: 593-604.

BRITO SL, MAIA-BARBOSA PM & PINTO-COELHO RM. 2016. Secondary productivity of main microcrustacean species of two tropical reservoirs in Brazil and its relationship with trophic state. J Limnol 75: 320-329.

BROOKS BW, LAZORCHAK JM, HOWARD MD, JOHNSON MV, MORTON SL, PERKINS DA, REAVIE ED, SCOTT GI, SMITH SA & STEEVENS AJ. 2016. Are harmful algal blooms becoming the greatest inland water quality threat to public health and aquatic ecosystems? Environ Toxicol Chem 35: 6-13.

BROWN JH, GILLOOLY JF, ALLEN AP, SAVAGE VM & WEST GB. 2004. Toward a metabolic theory of ecology. Ecology 85: 1771-1789.

BURNS CW. 1969. Relation between filtering rate, temperature, and body size in four species of Daphnia. Limnol Oceanogr 14: 693-700.

CABRAL JA & MARQUES JC. 1999. Life history, population dynamics and production of eastern mosquitofish, *Gambusia holbrooki* (Pisces, Poeciliidae), in rice fields of the lower Mondego River Valley, western Portugal. Acta Oecol 20: 607-620.

CHOUERI RB, MELÃO M DA GG, LOMBARDI AT & VIEIRA AAH. 2007. Effects of cyanobacterium exopolysaccharides on life-history of *Ceriodaphnia cornuta* SARS. J Plankton Res 29: 339-345.

DE-MEESTER L, STOKS R & BRANS KI. 2018. Genetic adaptation as a biological buffer against climate change : Potential and limitations. Integr Zool 13: 372-391.

DELL AI, PAWAR S & SAVAGE VM. 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. J Anim Ecol 83: 70-84.

DUVAL WS & GEEN GH. 1976. Diel feeding and respiration rhythms in zooplankton. Limnol Oceanogr 21: 823-829.

FORSTER J, HIRST AG & ATKINSON D. 2011a. How do organisms change size with changing temperature? The importance of reproductive method and ontogenetic timing. Funct Ecol 25: 1024-1031.

FORSTER J, HIRST AG & WOODWARD G. 2011b. Growth and development rates have different thermal responses. Am Nat 178: 668-678.

GAMA-FLORES JL, SALAS MEH, SARMA SSS, NANDINI S, ZEPEDAMEJIA R & GULATI RD. 2015. Temperature and age affect the life history characteristics and fatty acid profiles of *Moina macrocopa* (Cladocera). J Therm Biol 53: 135-142.

GAULD DT. 1951. The grazing rate of planktonic copepods. J Mar Biol Assoc United Kingdom 29: 695-706.

GELLER W. 1975. Die Nahrungsaufnahme von *Daphnia pulex* in Abhängigkeit von der Futterkonzentration, der Temperatur, der Körpergröße und dem Hungerzustand der Tiere. Arch Hydrobiol 48: 47-107.

GERKE P, BÖRDING C, ZEIS B & PAUL RJ. 2011. Adaptive haemoglobin gene control in *Daphnia pulex* at different oxygen and temperature conditions. Comp Biochem Physiol - A Mol Integr Physiol 159: 56-65.

GLADYSHEV MI, SUSHCHIK NN, DUBOVSKAYA OP, BUSEVA ZF, MAKHUTOVA ON, FEFILOVA EB, FENIOVA IY, SEMENCHENKO VP, KOLMAKOVA AA & KALACHOVA GS. 2014. Fatty acid composition of Cladocera and Copepoda from lakes of contrasting temperature. Fresh Biol 60: 373-386.

GOSS LB & BUNTING DL. 1980. Temperature effects on zooplankton respiration. Comp Biochem Physiol -- Part A Physiol 66: 651-658.

GOTELLI NJ & ELLISON AM. 2004. A primer of ecological statistics. Sunderland, Mass: Sinauer Associates Publishers, 2nd ed, 579 p.

GÜNTZEL AM, MATSUMURA-TUNDISI T & ROCHA O. 2003. Life cycle of *Macrothrix flabelligera* Smirnov, 1992 (Cladocera, Macrothricidae), recently reported in the Neotropical region. Hydrobiologia 490: 87-92.

HARDY ER. 1989. Effect of temperature, food concentration and turbidity on the life cycle characteristics of planktonic cladocerans in a tropical lake. Central Amazon: Field and Experimental work. London: University of London 12(2): 155-168.

HÉBERT MPP, BEISNER BE & MARANGER R. 2017. Linking zooplankton communities to ecosystem functioning: Toward an effect-Trait framework. J Plankton Res 39: 3-12.

HOEFNAGEL KN, DE VRIES EHJL, JONGEJANS E & VERBERK WCEP. 2018. The temperature-size rule in *Daphnia magna* across different genetic lines and ontogenetic stages: Multiple patterns and mechanisms. Ecol Evol 8: 3828-3841.

IPCC. 2014. Climate Change 2014: Synthesis Report. Contrib Work Groups I, II III to Fifth Assess Rep Intergov Panel Clim Chang Core Writ Team, Pachauri RK, Meyer LA IPCC, Geneva, Switzerland, 151 p.

JEPPESEN E ET AL. 2010. Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. Hydrobiologia 646: 73-90.

KOBAYASHI M. 1974. Oxygen consumption of *Daphnia magna*. Sci Reports Niigata Univ Ser D 11: 1-10.

KOOIJMAN SALM. 2000. Dynamic Energy and Mass Budgets in Biological Systems. 2nd ed, Cambridge: Cambridge University Press, 424 p.

KOOIJMAN SALM, HOEVEN N VAN DER & WERF DC VAN DER. 1989. Population consequences of a physio- logical model for individuals. Funct Ecol 3: 325-336.

KOTOV AA & BOIKOVA OS. 1998. Comparative analysis of the late embryogenesis of *Sida crystallina* (O.F. Müller, 1776) and *Diaphanosoma brachyurum* (Levin, 1848) (Crustacea: Brachiopoda: Ctenopoda). Hydrobiologia 380: 103-125.

LAMPERT W. 1977. Studies on the carbon balance of *Daphnia pulex* De Geer as related to environmental conditions. II. The dependence of carbon assimilation on animal size, temperature, food concentration and diet species. Arch Hydrobiol 48: 310-335.

LANG B, EHNES RB, BROSE U & RALL BC. 2017. Temperature and consumer type dependencies of energy flows in natural communities. Oikos 126: 1717-1725.

LANSAC-TÔHA F, BONECKER C, VELHO L, SIMÕES N, DIAS J, ALVES G & TAKAHASHI E. 2009. Biodiversity of zooplankton communities in the Upper Paraná River floodplain: interannual variation from long-term studies. Brazilian J Biol 69: 539-549.

LAZZARO X. 1987. A review of planktivorous fishes: Their evolution, feeding behaviours, selectivities, and impacts. Hydrobiologia 146: 97-167.

LOREAU M ET AL. 2001. Ecology: Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294(80): 804-808.

MASCLAUX H, BEC A, KAINZ MJ, PERRIÈRE F, DESVILETTES C & BOURDIER G. 2012. Accumulation of polyunsaturated fatty acids by cladocerans: effects of taxonomy, temperature and food. Fresh Biol 57: 696-703.

MASSARIN S, ALONZO F, GARCIA-SANCHEZ L, GILBIN R, GARNIER-LAPLACE J & POGGIALE JC. 2010. Effects of chronic uranium exposure on life history and physiology of *Daphnia magna* over three successive generations. Aquat Toxicol 99: 309-319.

MÜLLER H. 1972. Wachstum and phosphatbedarf von *Nitzschia actinastroides* (Lemn.) v. Goor in statischer und homokontiuierliecher kultur unter phosphatlimitierung. Arch Hydrobiol Suppl 38: 399-484.

O'CONNOR MI, PIEHLER MF, LEECH DM, ANTON A & BRUNO JF. 2009. Warming and resource availability shift food web structure and metabolism. PLoS Biol 7: 3-8.

PETRUSEWICZ K. 1967. Concepts in studies on the secondary produtivity of terrestrial ecosystems. In: Petrusewicz K (Ed), Secondary produtivity of terrstrial ecosystems. Warsaw: Panstwowe Wydawnictwo Naukowe, p. 17-49.

PÖRTNER HO & FARRELL AP. 2008. Physiology and Climate Change. Science 322: 690-692.

PÖRTNER HO & KNUST R. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315: 95-97.

R CORE TEAM. 2019. A Language and Environment for Statistical Computing. 2013. Vienna: R Foundation for Statistical Computing.

SABA GK, STEINBERG DK & BRONK DA. 2009. Effects of diet on release of dissolved organic and inorganic nutrients by the copepod *Acartia tonsa*. Mar Ecol Prog Ser 386: 147-161.

SARMENTO H, UNREIN F, ISUMBISHO M, STENUITE S, GASOL JM & DESCY JP. 2008. Abundance and distribution of picoplankton in tropical, oligotrophic Lake Kivu, eastern Africa. Freshw Biol 53: 756-771.

SAVAGE VM, GILLOOLY JF, BROWN JH, WEST GB & CHARNOV EL. 2004. Effects of Body Size and Temperature on Population Growth. Am Nat 163: 429-441.

SHURIN JB, CLASEN JL, GREIG HS, KRATINA P & THOMPSON PL. 2012. Warming shifts top-down and bottom-up control of pond food web structure and function. Philos Trans R Soc B Biol Sci 367: 3008-3017.

ŠORF M, DAVIDSON TA, BRUCET S, MENEZES RF, SØNDERGAARD M, LAURIDSEN TL, LANDKILDEHUS F, LIBORIUSSEN L & JEPPESEN E. 2015. Zooplankton response to climate warming: a mesocosm experiment at contrasting temperatures and nutrient levels. Hydrobiol 742: 185-203.

SOSNOVÁ M & KLIMEŠOVÁ J. 2009. Life-history variation in the short-lived herb *Rorippa palustris*: The role of carbon storage. Acta Oecol 35: 691-697.

TRAILL LW, LIM MLM, SODHI NS & BRADSHAW CJA. 2010. Mechanisms driving change: Altered species interactions and ecosystem function through global warming. J Anim Ecol 79: 937-947.

VERBERK WCEP, DURANCE I, VAUGHAN IP & ORMEROD SJ. 2016. Field and laboratory studies reveal interacting effects of stream oxygenation and warming on aquatic ectotherms. Glob Chang Biol 22: 1769-1778.

VISSER PM, VERSPAGEN JMH, SANDRINI G, STAL LJ, MATTHIJS HCP, DAVIS TW, PAERL HW & HUISMAN J. 2016. How rising CO2 and global warming may stimulate harmful cyanobacterial blooms. Harmful Algae 54: 145-159.

WEST DC & POST DM. 2016. Impacts of warming revealed by linking resource growth rates with consumer functional responses. J Anim Ecol 85: 671-680.

WINBERG GG, PECHEN GA & SHUSHKINA EA. 1965. The production of planktonic crustaceans in three different types of lake. Zool Zhurnal 44: 676-688.

YURISTA PM. 1999. Temperature-dependent energy budget of an Arctic Cladoceran, *Daphnia middendorffiana*. Freshw Biol 42: 21-34.

YURISTA PM. 2004. Bioenergetics of a semi-tropical cladoceran, *Daphnia lumholtzi*. J Freshw Ecol 19: 681-694.

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