



Thresholds and interactive effects of BPA-gradient and temperature on life history traits of *Daphnia magna*[☆]

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ABSTRACT

Bisphenol A (BPA), a synthetic organic compound widely used in the production of plastics, is recognized as an emerging contaminant because of its toxicity and the potential risks associated with bioaccumulation in organisms. Despite potential environmental hazards, there is a lack of studies examining BPA toxicity mechanisms and its potential impact on various trophic levels, with even fewer exploring whether global stressors such as temperature can affect the toxicity of BPA in organisms. Our aim was to assess the combined impact of BPA and varying temperature regimes on life-history traits in *Daphnia magna*. Our results revealed a significant impact of BPA on the growth, reproduction, and accumulated moulting of *D. magna*, with adverse effects primarily associated with the assimilation of BPA in algae rather than the BPA present in the medium, pointing to a trophic transfer mechanism. The interactive effect between BPA and temperature demonstrated a slight stimulatory effect of low BPA level on *D. magna* growth rate under warming constant conditions, but an inhibitory under warming fluctuating temperatures. Additionally, a BPA threshold was identified, below which growth became temperature-dependent. This study emphasizes the crucial role of considering temperature in predicting how toxins may affect *Daphnia* within aquatic food webs.

1. Introduction

Bisphenol A (BPA), a synthetic organic compound extensively employed in manufacturing plastics, polycarbonate, and thermal paper (Hoekstra and Simoneau, 2013), is commonly found in everyday items like water pipes, medical equipment, and packaging materials (Björnsdotter et al., 2017). With an estimated global annual production of 10 million tons in 2022 (Mishra et al., 2023), this ubiquitous compound along with other substances, is broadly recognized as endocrine-disrupting chemicals (EDCs) (Pojana et al., 2007; Theus et al., 2023). EDCs have the potential to disrupt the normal hormone function in wildlife and humans, causing morphological alterations, reduced fertility or reproduction (e.g. Levy et al., 2004; Oehlmann et al., 2006;

De Kermoyan et al., 2013).

Global concerns have been brought to the large variety of EDCs identified in underground waters, rivers, and lakes (Azizullah et al., 2022), as well as on aquatic biota (Berhane et al., 2017; Azizullah et al., 2022). In aquatic ecosystems, industrial and municipal wastewater are the predominant sources of BPA contamination (Azevedo et al., 2001; Gorga et al., 2015). Recognized as an emerging contaminant (Berhane et al., 2017), several countries have prohibited BPA in specific applications (Zheng et al., 2019; Mishra et al., 2023). For example, the European Union has implemented stricter regulations on both the production and application of BPA (Directive, 2011/8/EU; Directive, 2011/10/EU) prohibiting the use in infant bottles. Moreover, recent EFSA (Gundert-Remy et al., 2017) legislation regulated the BPA use in

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thermal paper and limited the permissible BPA concentration in drinking water to 20 ppb.

Despite regulatory measures, BPA concentrations remain significant in natural waters (Wu and Seebacher, 2020; Mishra et al., 2023). A comprehensive review of data concerning BPA contamination in these habitats indicates that, in most cases, BPA levels in fresh and marine waters were below $1 \mu\text{g L}^{-1}$ (Azizullah et al., 2022). Higher concentrations, however, have been reported in freshwater habitats (from 0 to $64 \mu\text{g L}^{-1}$; Belfroid et al., 2002; Wu and Seebacher, 2020), river and sea waters in Turkey ($4.62\text{--}29.92 \mu\text{g L}^{-1}$; Ozhan and Kocaman, 2019) surface water in Brazil ($0.02\text{--}13 \mu\text{g L}^{-1}$; Montagner et al., 2018), and in Danube River (reaching up to $130 \mu\text{g L}^{-1}$; www.lfu.bayern.de). Moreover, water resources near industrial and commercial cities typically exhibit elevated levels of BPA (Huang et al., 2012), with concentrations between 0.33 and $910 \mu\text{g L}^{-1}$ (Wang et al., 2019; Tappert et al., 2023).

Although the half-life of BPA is reported to be very short in surface water under aerobic conditions (3–6 days; Klečka et al., 2001), the continuous exposure and potential persistence of BPA and its derivatives contributes to their overall toxicity (e.g. Faisal Manzoor et al., 2022; Rybczyńska-Tkaczyk et al., 2023). In fact, numerous studies have confirmed its accumulation in the bodies of aquatic organisms (Corrales et al., 2015), with examples documented in algae, amphibians, annelids, crustaceans, fish, and rotifers, among others (Corrales et al., 2015; Guo et al., 2017; Li et al., 2018). However, most experiments conducted used BPA concentrations one or two orders of magnitude higher than those found in natural ecosystems, ranging from 1 to 50mg L^{-1} (e.g. Gerhardt, 2019; Esperanza et al., 2020; Chen et al., 2021) and, in some cases, reaching gram-per-liter concentrations (De Kermoyan et al., 2013). Performing experiments with naturally occurring BPA concentrations is crucial for accurately assessing the true impact of this toxin on species. Moreover, there are large gaps in understanding BPA assimilation in algae and their effect on consumer (Granek et al., 2020).

Beyond the significance of BPA and EDCs for both environments and human health, climate change is reshaping entire ecosystems impacting the living organisms within them (Prakash, 2021). Projections for ongoing global climate change suggest a potential elevation in global surface temperatures from 1.5 to $5.8 \text{ }^\circ\text{C}$ by the end of the twenty-first century, accompanied by increased thermal fluctuations (IPCC et al., 2022) and a forecasted rise in the frequency and intensity of extreme events (Bindoff et al., 2013). Consequently, this poses a significant threat to the global environment, biodiversity and sustainable human development (Huang et al., 2021).

This projected change in climate will place additional stress on already-burdened freshwater and coastal ecosystems. Although aquatic systems are typically perceived as resilient, rapid climate change may impose new environmental conditions that surpass the resilience thresholds (LeRoy Poff et al., 2002). For example, the anticipated prolonged warming periods in aquatic systems (O'Reilly et al., 2015; Woolway and Merchant, 2019) imply that freshwater organisms will encounter persistent elevated temperatures concurrently with other environmental stressors such as chemical contaminants (Polazzo et al., 2022). These interactions may result in non-additive responses, creating greater (synergistic) or lesser (antagonistic) effects than those expected from the single stress acting separately (Birk et al., 2020; Carrier-Belleau et al., 2023).

The interconnected crises of plastic pollution and climate change, although often studied separately, co-occur, posing a threat to habitat resilience by significantly heightening organisms' sensitivity to toxicants (López-Valcárcel et al., 2023), resulting in changes to community composition, ecosystem function, and biogeochemical cycles (Ford et al., 2022). Thus, it has been shown that temperature increases BPA toxicity in fish to reduce thermal tolerance (Little and Seebacher, 2015). Although other similar studies have illustrated the combined impact of both global (climate change) and local (pollution) processes on organisms such as phytoplankton (Theus et al., 2023), cladocerans (Jaikumar et al., 2018), and snails (Oehlmann et al., 2006), predicting the scaling

effects in food webs demands more complex experiments involving a minimum of two trophic levels (Granek et al., 2020).

In freshwater habitats, zooplankton plays a key role by maintaining water transparency, reducing concentrations of detritus and suspended solids (Jeppesen et al., 1999), and by their fundamental involvement in nutrient cycles and energy fluxes (Bruce et al., 2006; Suhett et al., 2015). Cladocerans, in particular, have distinctive biological features that render them valuable in experimental studies. Inhabiting highly variable environments (Dodson et al., 2009), they serve as an informative model for investigating responses to environmental stress and are extensively employed in toxicological research (e.g. Steinberg et al., 2010; López-Valcárcel et al., 2023). Given these attributes, the *Daphnia* genus is highly regarded as an ecological model for generalist filter feeders, with variations in water temperature directly influencing their physiology, metabolism, and behaviour (Giebelhausen and Lampert, 2001; Brown et al., 2004), thereby impacting the balance of aquatic ecosystems.

This study aimed to assess the impact of naturally occurring concentrations of BPA and varying temperature conditions on a set of life history traits in *D. magna*. This assessment involved examining the combined effects of BPA in food and varying temperature conditions on growth, moulting, and reproduction of *D. magna*.

The following hypotheses seek to shed light on the aforementioned gaps in understanding the impacts of BPA in aquatic systems.

- (1) the growth rate (GR) and other life-history traits of *D. magna*, are negatively affected by BPA, and this detrimental effect is predominantly influenced by the BPA content present in its food rather than BPA in the medium
- (2) the magnitude of adverse effects of BPA on the GR of *D. magna* is affected by temperature, with more pronounced effects in warming-constant temperature (WCT) scenarios relative to warming-fluctuating temperature (WFT) scenarios.

2. Materials and methods

2.1. Culturing algae and *Daphnia magna*

The strain of *Scenedesmus* sp. (designated Ida Sce/RS) was originally isolated from Río Seco Lake in Sierra Nevada and has been maintained for over 10 years in exponentially growing semicontinuous batch culture with COMBO ATE medium (Kilham et al., 1998) in the culture collection at the Granada University Institute of Water Research (see Ramos-Rodríguez et al., 2022). *Scenedesmus* sp. was cultured in 0.6 L volume in the isolated room at $17.5 \pm 0.7 \text{ }^\circ\text{C}$ with sterile-filtered air and $\sim 100 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ PAR on a 15 h:9 h light: dark cycle. Exponential growth was maintained by harvesting 50% of the volume of the culture weekly and replacing it with a new COMBO ATE medium to bring the culture to the original volume (following Ramos-Rodríguez et al., 2022).

The adults and neonates of *D. magna* required for the experiments originated from a uniclinal stock culture of *D. magna* provided by the University of Jaén (Spain), sampled from Laguna Grande (Jaén, Spain) that had been successfully maintained for several months at the Institute of Water Research at the University of Granada. *D. magna* was grown in COMBO ANIMATE medium (Kilham et al., 1998) in aquariums at two different temperatures of $19 \pm 1 \text{ }^\circ\text{C}$ and $22 \pm 1 \text{ }^\circ\text{C}$, with $\sim 90 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ photosynthetically active radiation (PAR) on a 12:12 light: dark cycle. The organisms were fed *ad libitum*, approximately $4 \times 10^5 \text{ cells ml}^{-1}$ of *Scenedesmus* sp. ($\sim 5 \text{ mg C L}^{-1}$) three times a week.

We conducted three separate experiments to assess the potential effects of BPA-Food on *D. magna*, and the interaction between high constant and high fluctuating temperature regimes \times BPA-Food gradient as described below.

2.2. BPA exposure experiment

To ascertain whether the impact of BPA on the response of *D. magna* is attributed to BPA by exposure in medium (waterborn route) or BPA contained in the food (dietary route), we conducted a full 2×5 factorial experiment, employing two factors (i) “BPA food” with two levels, food (*Scenedesmus* sp.) cultured in medium without BPA (-BPA food) and with BPA (+BPA food), and (ii) “BPA-gradient” with five levels of BPA concentration (0, 5, 10, 50, and $100 \mu\text{g L}^{-1}$ of BPA; See Fig. 1) added to COMBO ANIMATE culture medium. BPA concentrations were prepared by dissolving the pure compound (99%, Sigma-Aldrich, Madrid-Spain) in Dimethyl sulfoxide (DMSO; Sigma Aldrich).

All the culture-batch of *Scenedesmus* sp. to feed *D. magna* grew in the BPA-gradient indicated previously under light continuous conditions (i. e. 24 h: 0 h light: dark), and aerators were installed to prevent algal sedimentation and to maximize algal growth rate. After eight days, *Scenedesmus* sp. cell abundance was estimated from each BPA-gradient in both levels of “BPA food” treatments by counts in Neubauer chambers under binocular microscope. Harvested algae were stored in a refrigerator at 4°C and were used to feed *D. magna* cultures during the BPA exposure experiment.

In parallel, *D. magna* individuals were cultured for a minimum of two generations and selected from at least the third clutch before commencing the trials (Sakwinska, 2004), avoiding the maternal effects in the life history experiments, and reducing variability among test animals.

The BPA exposure experiment was conducted in 80 ml capacity glass tubes, where each level of treatment was replicated five times (total $n = 50$) and the treatments were combined as shown in Fig. 1. In each tube, one neonate (organisms born within less than 24 h; density of 17 individuals per liter) was introduced with 60 ml of culture medium. Experiments were carried out in a room with a controlled temperature of 22°C and a 12:12 light-to-dark photoperiod. Daily monitoring of treatments was performed to record ovarian development, moulting occurrences, and the presence of gravid females. Each day, organisms were fed with the *Scenedesmus* sp. at a density of 5×10^5 cells mL^{-1} (Alvarez et al., 2022) which was cultivated at each specific BPA-gradient. This food concentration has been determined to be optimal for maintaining the population’s health (e.g. Nandini and Sarma, 2003). The organisms were transferred to a new tube with fresh-culture medium daily to prevent them from experiencing starvation. The experiment concluded when the first *D. magna* individual became gravid, which occurred at 5th day.

To estimate somatic growth, before starting the experiment, ten neonates were pipetted into pre-weighed aluminum cups, which were weighed after 48 h at 60°C using a Mettler ultramicrobalance (with a precision $\pm 0.1 \mu\text{g}$, Mettler, Germany) to determine their initial body weight. At the end of the experiment, each *D. magna* was transferred into pre-weighed aluminum cups, which were weighed after 48 h at 60°C . The somatic growth rate (GR) was calculated as follows:

$$\text{GR} = (\ln M_t - \ln M_o) / t$$

where M_t is the final body mass, M_o is the initial body mass and t is the time (in days) at which animals were collected for their weight. In the cases where organisms died before the conclusion of the experiment, the GR was calculated by dividing the body mass by the specific number of days the organisms remained alive.

2.3. Interactive BPA food \times temperature experiment

Considering that the GR of *D. magna* was mainly impacted by BPA transferred through food (dietary route, see Results), we conducted two new experiments to evaluate the BPA food effect on the GR, moulting and reproduction of *D. magna* under increased constant temperature and fluctuating temperature.

For the first experiment, warming constant temperature (“WCT”), we employed a full 2×8 factorial design with two factors (i) “warming”, with two levels: Control (C, 19°C) and warming-constant (WC, 24°C), and (ii) “BPA food” with eight levels (0, 5, 10, 50, 100, 350, 650, $1000 \mu\text{g L}^{-1}$) (Fig. 2), adding the corresponding BPA concentrations to medium COMBO ANIMATE in which *D. magna* was exposed and fed with *Scenedesmus* sp. grown along the same BPA-gradient.

For the second experiment, warming fluctuating temperature (“WFT”), we conducted a 2×8 factorial design with two factors (i) “fluctuation”, with two levels: Control (C, 19°C) and warming-fluctuating (WF, fluctuating 19°C - 24°C in 12-h cycles) and (ii) “BPA food” with eight levels identical to those in the previous experiment. For the WF treatments, each shifting period of 5°C of amplitude lasted 12 h and was gradual. The warming phase (from 19 to 24°C) was synchronized with the light hours, and the cooling phase (from 24 to 19°C) with dark hours.

Each experiment was conducted in two rooms designed to maintain controlled specific temperatures (C, WC, WF). For each treatment, which was replicated 5 times, 80 ml capacity glass tubes were used (totaling $n = 80$ for each experiment). In each of these tubes, one neonate

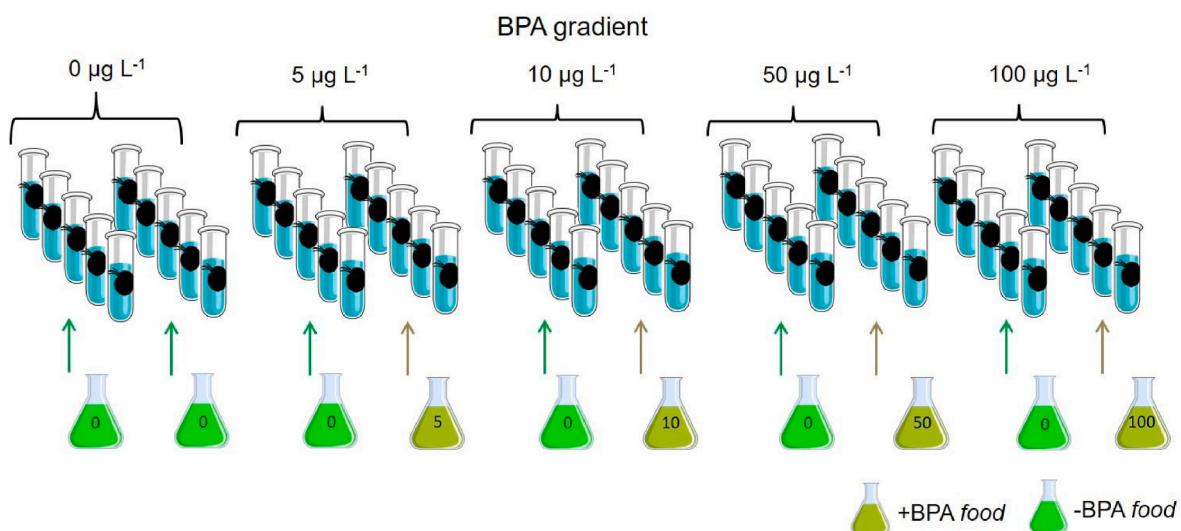


Fig. 1. Schema illustrating the methodology used in the BPA exposure experiment with two factors: “BPA food” (+BPA food and -BPA food) and “BPA-gradient” (0, 5, 10, 50 and $100 \mu\text{g L}^{-1}$ of BPA).

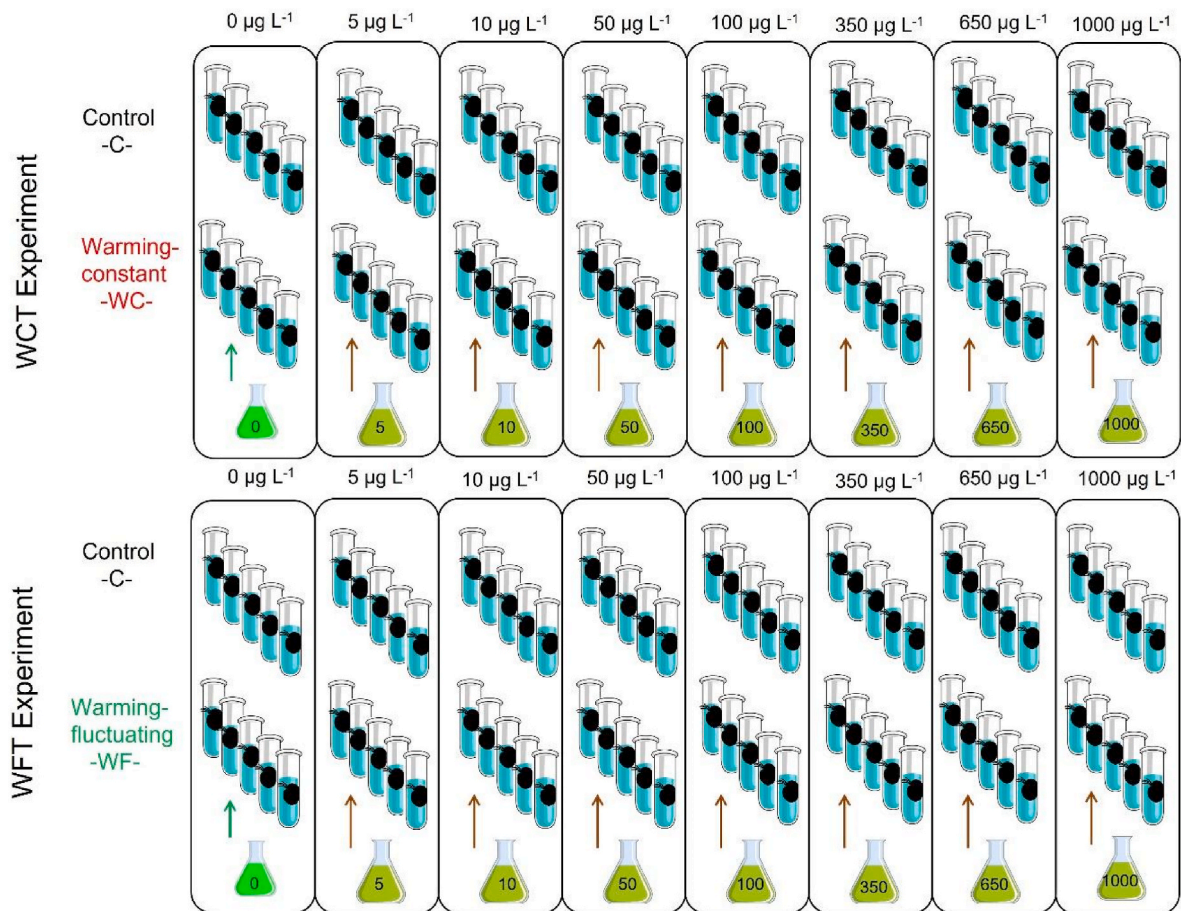


Fig. 2. Schema illustrating the methodology used in the warming-constant temperature experiment (WCT) and the warming-fluctuating temperature experiment (WFT), each experiment with two factors: “BPA food gradient” and “warming” or “fluctuation”.

(organism with a lifespan of less than 24 h) from clones maintained at 19 °C was introduced with 60 ml of culture medium, following the scheme described in Fig. 2. All tubes were incubated in an aquaria system equipped with adjustable temperature by refrigeration (Teco® TK2000, EU) and with radiation from light-emitting diode lamps (nano LED light v.2.0, BLAU aquaristic, EU) for PAR (12:12 light to dark photoperiod).

The organisms were fed with 5×10^5 cells ml⁻¹ of *Scenedesmus* sp. The growth of algae cultures occurred under continuous light conditions (i.e. 24 h:0 h light:dark; as described in the previous section), with specific BPA concentrations (0, 5, 10, 50, 100, 350, 650, and 1000 µg L⁻¹). The harvested algae were stored in a refrigerator at 4 °C and were used to feed *D. magna* during experiments.

In line with the previous experiment, organisms were transferred daily to new culture media to avoid starvation, and the experiment concluded once the first individual of *D. magna* produced its initial clutch, which occurred at 5th day. Daily monitoring of treatments was performed to record ovarian development, moulting occurrences, and the presence of gravid females. Somatic growth rate was calculated as previously described.

2.4. BPA assimilated by *Scenedesmus* sp.

Three samples of 1 ml were collected for each food concentration (i.e. 0, 5, 10, 50, 100, 350, 650, and 1000 µg L⁻¹) each day of the experiments and filtered onto pre-combusted (1 h at 550 °C) glass-fiber filters (Whatman GF/C). The filters were stored at -5 °C, and the filtered water was preserved at 4 °C up to the determination of BPA concentration.

For BPA analysis each sample (1 mL) was placed in a 1.5 mL tap-cap polypropylene Eppendorf tube. Next, 100 µL of 40% NaCl solution were added, and vortexed for 20 s, and 300 µL⁻¹ of a mixture consisting in acetonitrile: trichloromethane 1:3 (2.5% formic acid) was added. The resulting solution mixture was gently shaken by vortex for 60 s and centrifuged for 5 min at 13,000 rpm. All sedimented phase volume was transferred to a clean glass vial. The organic phase was evaporated under a nitrogen stream. The residue was dissolved with 100 µL⁻¹ of a mixture consisting of acetonitrile–water 70:30 (v/v), and it was vortexed for 30 s, before injection into the LC-MS/MS system.

LC-MS/MS analyses were conducted with a NexeraXR LC-20A liquid chromatography instrument (Shimadzu, Japan) and a QTRAP MS/MS4500 mass spectrometer (AB Sciex, Framingham, MA). Procedural blanks were analyzed to control for background contamination, and no quantifiable concentrations of BPA were detected. In addition, Milli-Q water spiked at 5 ng g⁻¹ and 1000 ng g⁻¹ was injected in triplicate every 15 injections. BPA assimilated by algae was estimated as the differences between the BPA added to each culture medium and the BPA measured in the water.

2.5. Food quantity and quality

To assess potential changes in food quantity and quality throughout the experiment three samples of 1 ml were collected for each food concentration (i.e. 0, 5, 10, 50, 100, 350, 650, and 1000 µg L⁻¹) and filtered onto pre-combusted (1h at 550 °C) glass-fiber filters (Whatman GF/C) at low pressure (<100 mmHg). The filters were stored at -5 °C. The C and N content in the filters containing algae were analyzed using an elemental analyzer (PerkinElmer 2400 CNH), while for P content,

filters were introduced into acid-washed vials, digested with a mixture of potassium persulfate and boric acid at 120 °C for 30 min, and determined as SRP in 10 cm quartz cuvettes via acid molybdate technique (APHA, 2012). Blanks and standards were performed for all procedures. All C:P and C:N ratios were calculated on a molar basis.

2.6. Data analysis

For each experiment, the effect size of BPA on GR was calculated as:

$$\text{Effect size of BPA} = (X_i - C) / C$$

Where X_i is the GR of *D. magna* in each BPA concentration and C is the GR in the control treatment for each experiment.

In each experiment, two-way ANOVA was used to test the effects of the factors (BPA food and BPA-gradient in BPA exposure experiment, and warming or fluctuation and BPA-Food gradient in WCT and WFT experiments) on GR of *D. magna*, BPA effect size on GR of *D. magna* and total number of accumulated moults. Additionally, we assessed the variation in BPA assimilation by algae over time through a one-way repeated-measures RM-ANOVA.

In all analyses when the interaction term was significant, post-hoc Tukey tests were conducted to test significant differences between treatments. Normality of residuals and homoscedasticity of data were assessed using the Shapiro-Wilk and Cochran tests, respectively (Zar, 1999). In cases where an assumption was not met, standard data transformations were applied. If the data transformation failed to rectify the deviation from the assumptions, the ANOVA was conducted on the original untransformed data but considering a more conservative significance level ($\alpha = 0.01$). By applying this restriction, we reduced the likelihood of committing a Type I error (Zar, 1999; Quinn and Keough, 2002), and assumed that the ANOVA results remained robust despite the departure from the assumptions (Underwood, 1997). For RM ANOVA, in cases of departure of sphericity (Mauchly Sphericity Test), we applied the Greenhouse–Geisser Epsilon (GGE) adjustment to the degrees of freedom (Von Ende, 2001).

The WC or WF effect along the BPA-assimilated by algae gradient (covariate) was assessed by analysis of covariance. The interaction between each temperature (WC or WF) and the covariate was graphically determined by examining the slopes and the 95% confidence intervals of the regression lines; the level of the covariate where these intervals overlap provides the threshold where temperature effect arises or vanishes.

Statgraphics Centurion XVI 16.0.07 (Manugistics Inc., Rockville, MD) and Statistica 5.1 (StatSoft GmbH, Germany) were used for statistical analyses.

3. Results

The results of each experiment are presented in the in the chronological sequence of biological events observed in organisms. Initially, organisms experience growth (in our case, growth rate: GR) to increase in size. Subsequently, they undergo successive moulting (accumulated moults) before reaching adulthood and reproducing (gravid female percentage in our case).

3.1. BPA exposure effects

The results aimed to assess whether the effects of BPA on *D. magna* are influenced by food (dietary route) or by BPA present in the medium (waterborne route) revealed that the GR of *D. magna* was significantly higher (average 20%) in organisms fed *Scenedesmus* sp. without BPA (-BPA food; waterborne route) compared to those fed with BPA (+BPA food; dietary route), as indicated by the significant main effect of BPA food (Table 1). Notably, the GR of *D. magna* increased at a BPA concentration of 5 $\mu\text{g L}^{-1}$ under -BPA food but decreased along the BPA-gradient. However, this positive response was not observed under +

Table 1

Results to two-way ANOVA on growth rate (GR) of *Daphnia magna*, effect size of BPA on GR and number of accumulated moults in a) BPA exposure experiment, b) warming-constant temperature (WCT) experiment and c) warming-fluctuating temperature (WFT) experiment.

a) BPA exposure	Effect	SS	Df	F	p
Growth rate	BPA-gradient	0.010	4	2.843	0.036*
	BPA food	0.006	1	7.155	0.010*
	BPA-gradient \times BPA food	0.003	4	0.979	0.430
	Error	0.035	39		
Effect size	BPA-gradient	0.145	3	3.26	0.03*
	BPA food	0.131	1	8.85	0.00**
	BPA-gradient \times BPA food	0.028	3	0.63	0.598
	Error	0.473	32		
Accumulated moults	BPA-gradient	2.06	4	0.83	0.51
	BPA food	2.46	1	3.95	0.05
	BPA-gradient \times BPA food	1.51	4	0.61	0.66
	Error	24.35	39		
b) WCT					
Growth rate	BPA food	0.926	7	64.21	0.00**
	Warming	0.105	1	51.27	0.00**
	BPA food \times Warming	0.062	7	4.281	0.00**
	Error	0.129	63		
Effect size	BPA food	6.792	6	65.06	0.00**
	Warming	0.009	1	0.556	0.45
	BPA food \times Warming	0.157	6	1.151	0.19
	Error	0.956	55		
Accumulated moults	BPA food	55.6	7	24.35	0.00**
	Warming	9.8	1	28.51	0.00**
	BPA food \times Warming	1.8	7	0.748	0.63
	Error	22	64		
c) WFT					
Growth rate	BPA food	1.328	7	124.1	0.00**
	Fluctuation	0.046	1	30.52	0.00**
	BPA food \times Fluctuation	0.022	7	2.063	0.06
	Error	0.097	64		
Effect size	BPA food	7.277	6	105.1	0.00**
	Fluctuation	0.024	1	2.117	0.15
	BPA food \times Fluctuation	0.050	6	0.725	0.63
	Error	0.646	56		
Accumulated moults	BPA food	5	7	35.26	0.00**
	Fluctuation	5	1	16.32	0.00**
	BPA food \times Fluctuation	5	7	2.33	0.034*
	Error	19.6	64		

SS is Sums of Squares, Df Degrees of freedom, F-test results. Significance level * $p < 0.05$ and ** $p < 0.01$.

BPA food (Fig. 3A), and the difference, although notable, was not significant enough to trigger an interaction between BPA food and BPA gradient (Table 1). Similarly, the mean effects size of BPA on GR was positive along the BPA-gradient in -BPA food treatment (except at 100 $\mu\text{g L}^{-1}$), and conversely, was negative in the +BPA food treatments (except at 5 $\mu\text{g L}^{-1}$), underscoring the adverse impact of BPA in the food (Table 1; Fig. 3B).

The number of accumulated moults showed no significant differences between BPA food and BPA-gradient treatments, suggesting the absence of significant single and interactive effects of these factors on this response variable (Table 1). Throughout the experiment, 80–100% of female feed with algae without BPA (-BPA food) were gravid, while in food with BPA (+BPA food), the percentage of gravid females decreased between 40 and 60%, respectively (Figs. S1 and A).

3.2. Interactive BPA food \times temperature effects

Given that the previous experiment demonstrated that *D. magna* was mainly affected by BPA transferred through food (dietary route), we evaluated this effect under two potential climate change scenarios: constant warming temperature and fluctuating warming temperature.

In a warming constant (WC) temperature experiment, the GR of

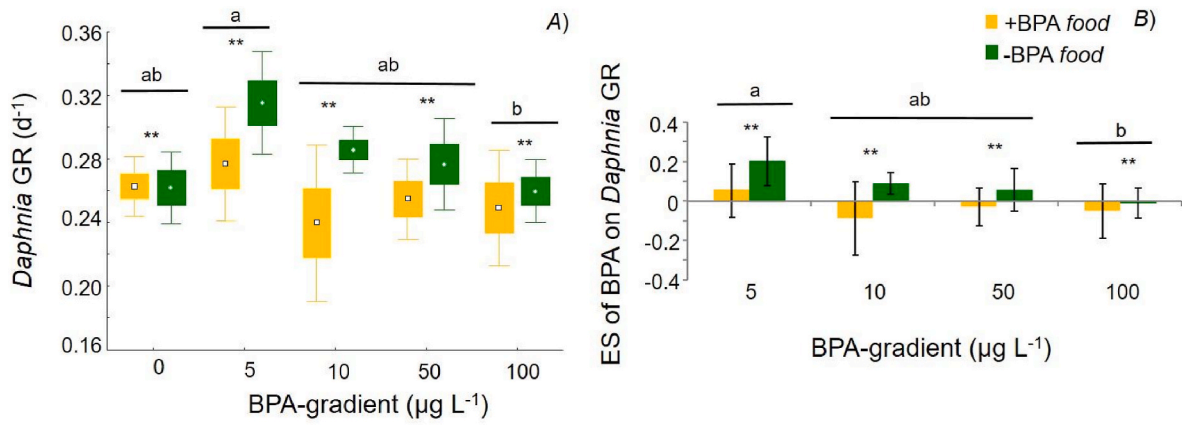


Fig. 3. A) Growth rate (GR, d^{-1}) of *D. magna* along BPA-gradient and B) the effect size (ES) of BPA on *D. magna* GR in BPA exposure experiment. Different lower-case letters illustrate differences between treatments along BPA-gradient in descendant order. Asterisks (**) illustrate differences between + BPA food and -BPA food treatment. In the A panel symbols within the boxes denote the mean, the boxes denote \pm SE, whiskers denote mean \pm SD.

D. magna peaked at 5, 10, and 50 $\mu g L^{-1}$ BPA food gradient under WC condition, but beyond 100 $\mu g L^{-1}$, differences between control (19 °C, C) and WC treatments were not significant (Fig. 4A), resulting in an interactive BPA food gradient \times WC effect (Table 1). Moreover, the GR of *D. magna* decreased by up to 90% compared to control (0 $\mu g L^{-1}$) in high BPA food concentrations (i.e. 650 $\mu g L^{-1}$ and 1000 $\mu g L^{-1}$), regardless of the temperature conditions (Fig. 4A). Noticeably, the effect size of BPA food gradient on the GR of *D. magna* was predominantly negative, with its magnitude increasing along the BPA-gradient in both temperature conditions; however, it was slightly positive at low BPA food concentrations (5 and 10 $\mu g L^{-1}$) under WC conditions (Fig. 4B; Table 1).

Daphnia magna died after three or four days when exposed to 1000 $\mu g L^{-1}$ of BPA in both temperature conditions.

The number of accumulated moults was significantly higher under WC than at C conditions (Fig. 4C), except for the BPA food gradient of 1000 $\mu g L^{-1}$, where significantly lower values were found for both C and WC conditions (Table 1). The WC regime promoted favorable conditions for the reproductive traits, leading to a 100% proportion of gravid females at BPA food concentrations ranging from 0 to 50 $\mu g L^{-1}$. However, this proportion decreased by 20 and 40% at BPA food concentrations of 100 and 350 $\mu g L^{-1}$, respectively, reaching zero at 650 and 1000 $\mu g L^{-1}$. Conversely, at the control temperature, no gravid females were recorded

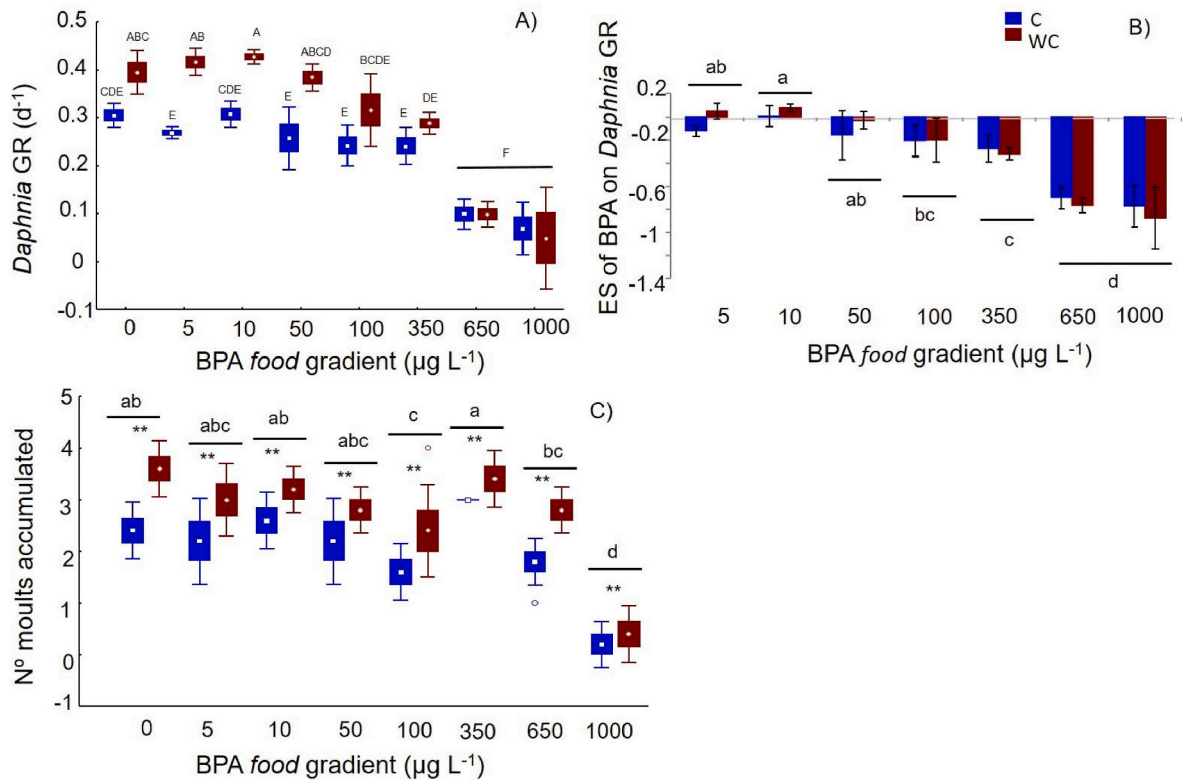


Fig. 4. Results of warming-constant temperature (WCT) experiment regarding to A) the growth rate (GR, d^{-1}) of *D. magna* along the BPA food gradient, B) the effect size (ES) of BPA food gradient on the GR of *D. magna* and C) the number of accumulated moults along the BPA food gradient. In panel A and C symbols within the boxes denote the mean, the boxes denote \pm SE, and whiskers denote mean \pm SD. Different lower-case letters illustrate differences between treatments along BPA food gradient in descendant order. Asterisks (**) illustrate differences between WC and C temperature and different capital letters illustrate differences with interactions between BPA food gradient \times temperature.

(Figs. S1 and B).

In the subsequent experiment involving warming fluctuating (WF) temperature, the GR of *D. magna* decreased between 45 and 95% at higher BPA food concentrations (i.e. 350, 650, and 1000 $\mu\text{g L}^{-1}$ BPA) compared to the 0 $\mu\text{g L}^{-1}$ BPA treatment (Table 1; Fig. 5A). Moreover, the GR of *D. magna* was significantly higher (up to 20%) in WF compared to the C condition. The effect size of BPA food on the GR of *D. magna*, was consistently negative along BPA food gradient in both temperature conditions (Fig. 5B). The magnitude of the negative effect size of BPA food on GR increasing at 650 $\mu\text{g L}^{-1}$ and 1000 $\mu\text{g L}^{-1}$ (Fig. 5B), resulted in a significant BPA-Food main effect (Table 1).

An interactive effect between BPA food and WF was observed on the number of accumulated moults (Table 1), with the highest values occurring at BPA food of 5 $\mu\text{g L}^{-1}$ under WF condition and the minimum at BPA food of 1000 $\mu\text{g L}^{-1}$ for both temperature conditions (Fig. 5C). The WF condition increased the proportion of gravid females, reaching values between 80 and 100% at BPA food concentrations ranging from 0 to 100 $\mu\text{g L}^{-1}$. However, this percentage decreased to 40% at BPA food concentration of 350 $\mu\text{g L}^{-1}$, reaching zero at BPA food concentrations of 650 and 1000 $\mu\text{g L}^{-1}$. Under C temperature, only 40% of females were detected as gravid at a BPA food concentration of 0 $\mu\text{g L}^{-1}$; for all other BPA food levels, the proportion was zero (Figs. S1 and C).

3.3. BPA assimilated by *Scenedesmus sp.* and temperature

The assessment of BPA concentration assimilated by *Scenedesmus sp.*

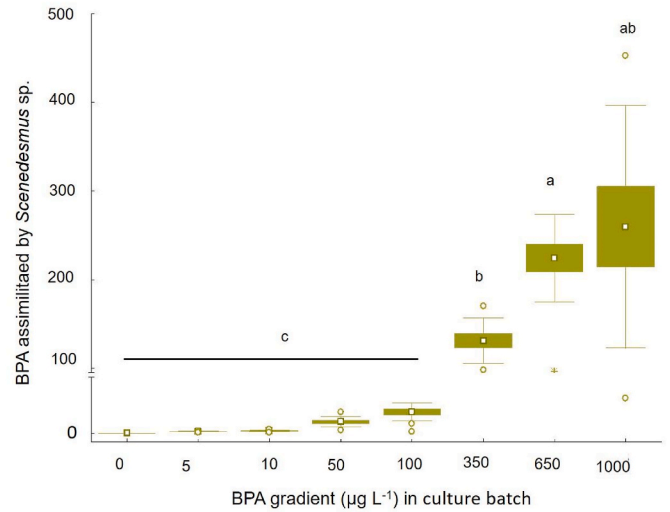


Fig. 6. BPA concentration assimilated by *Scenedesmus sp.* measured in each culture batch (BPA-gradient) during the temperature experiment run. Symbols within the boxes denote the mean, the boxes denote \pm SE, and whiskers denote mean \pm SD. Different lower-case letters illustrate differences between treatments.

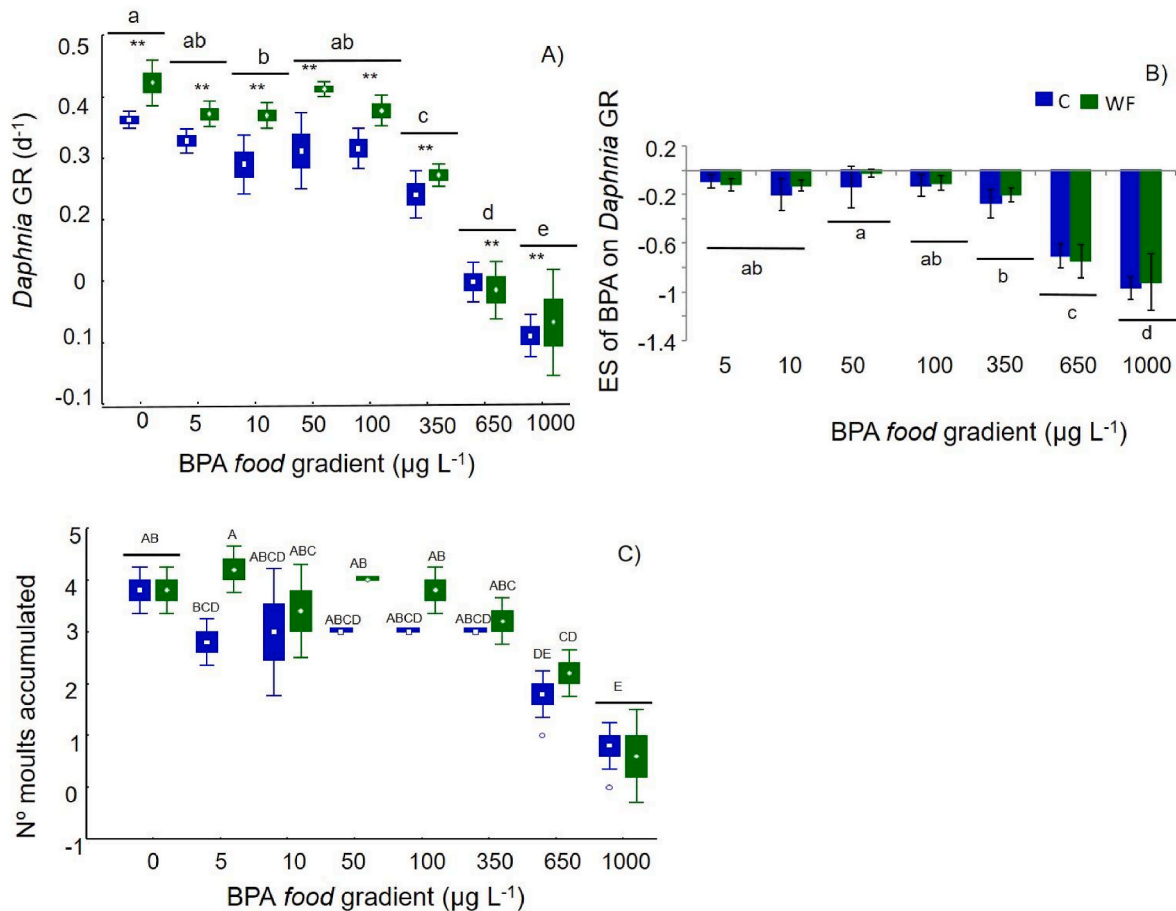


Fig. 5. Results of warming-fluctuating temperature (WFT) experiment regarding to A) the growth rate (GR, d^{-1}) of *D. magna* along the BPA-Food gradient, B) the effect size (ES) of BPA-Food gradient on the GR of *D. magna* and C) the number of accumulated moults along the BPA-Food gradient. In panel A and C symbols within the boxes denote the mean, the boxes denote \pm SE, and whiskers denote mean \pm SD. Different lower-case letters illustrate differences between treatments along BPA food gradient in descendant order. Asterisks (**) illustrate differences between WF and C temperature and different capital letters illustrate differences with interactions between BPA food gradient \times temperature.

ranged between 18 and 35% of the initially added BPA for all concentrations (Fig. 6). The highest levels of the BPA-assimilated by algae were found at BPA levels of $650 \mu\text{g L}^{-1}$ and $1000 \mu\text{g L}^{-1}$, and these levels differed significantly from all other concentrations (Fig. 6; RM-ANOVA, main effect of BPA-gradient $F_{7,32} = 13.85$, $p < 0.001$). No BPA \times Time interaction ($F_{28,32} = 1.35$, $p = 0.2$) nor an effect of the time ($F_{4,32} = 0.75$, $p = 0.56$) was found (Fig. S2), indicating that BPA-assimilated by algae remained stable over the days of storage.

To assess the impact of temperature conditions (WC or WF) across the BPA-assimilated by algae, we depicted a scatterplot illustrating the GR of *D. magna* against BPA-assimilated by *Scenedesmus* sp. (Fig. 7). The GR of *D. magna* showed a negative trend with increasing BPA-assimilated by algae. The temperature regime interacted with BPA-assimilated by algae revealing a BPA threshold, below which *Daphnia* growth was temperature-dependent, with positive effects of WC and WF on GR. This threshold was slightly lower under WF than WC ($100 \mu\text{g L}^{-1}$ for WF and $150 \mu\text{g L}^{-1}$ for WC), as indicated by the overlapping 95% confidence bands between the temperature conditions above each BPA-assimilated threshold (Fig. 7).

3.4. Food quantity and quality

Food quantity, measured in terms of C, ranged from 18 to 120 mgC L^{-1} , surpassing the minimum threshold of 0.7 mgC L^{-1} required for the growth of *Daphnia* (Lampert, 1976), thereby excluding the possibility of C-limitation. Furthermore, the C:P ratio in all BPA-Food levels ranged from 22 to 5, consistently below the critical threshold of 300 (Urabe et al., 1997), beyond which *D. magna* GR tends to decrease (Park et al., 2002).

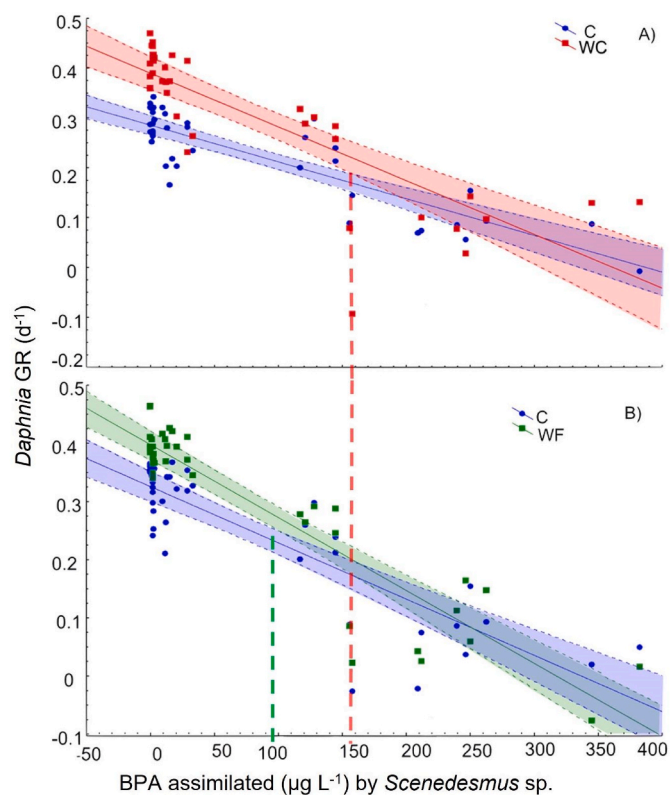


Fig. 7. Scatterplot of *D. magna* growth rate (GR) vs. BPA concentration assimilated by *Scenedesmus* sp. in A) warming constant temperature experiment (WCT) and in B) warming-fluctuating temperature experiment (WFT). Dashed vertical lines represent thresholds identified by overlapping confidence band for WCT (red) and WFT (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

This study addresses a knowledge gap regarding the impact of the interplay between climatic and chemical stressors on consumer populations in freshwater ecosystems (Polazzo et al., 2022). Our experiments encompassed a wide range of BPA concentrations, from environmentally realistic exposure levels to higher concentrations commonly utilized in laboratory studies. These were complemented by daily thermal fluctuations anticipated in future warming scenarios for freshwater ecosystems (IPCC et al., 2022). Our results demonstrate that (i) an increasing concentration of BPA, adversely affected the GR of *D. magna* along with other life traits, with the main negative effect mediated by BPA-assimilated by algae; (ii) BPA concentrations exceeding $350 \mu\text{g L}^{-1}$ resulted in a duplicated negative effect size on the GR of *D. magna* (i.e. $> 50\%$ inhibition) (iii) at low BPA concentrations, the effect size of BPA on the GR was stimulatory under WC (antagonistic interaction) while inhibitory under WF; (iv) warming revealed a threshold of BPA-assimilated by algae, slightly differing for WC or WF, below which *Daphnia* growth was temperature-dependent. These results have important implications, as explained in the following paragraphs:

Firstly, and consistently with our first hypothesis, the trophic transfer of BPA emerged as the primary pathway boosting the detrimental effects of BPA on the GR, reproduction, and survival of *D. magna*. In line with the findings of previous studies (Hirooka et al., 2005; Ji et al., 2014; Li et al., 2009), our research demonstrates that algae can uptake BPA from the aqueous medium and rapidly accumulate it during their growth. In fact, the concentration of assimilated BPA by *Scenedesmus* sp. ranged from 18 to 35%, values that remained steady throughout the experiment, and surpass values reported in other studies (e.g. 2–4%: Ben Ouada et al., 2018; 8–20%: Ji et al., 2014; Li et al., 2009). Additionally, our results indicated that the harmful impact of BPA on the GR of *D. magna* manifested earlier when BPA was assimilated by algae, starting at $5 \mu\text{g L}^{-1}$, whereas a higher BPA-concentration was required (i.e. $50 \mu\text{g L}^{-1}$) to trigger negative effects on GR when BPA was only present in the medium. Thus, this impact was primarily contingent on the presence of the contaminant in food, a pattern also observed in other zooplankton organisms (e.g. Magnusson et al., 2007; Guo et al., 2017).

Aquatic organisms primarily accumulate pollutants in their bodies through two main routes: filtering the surrounding water (waterborne route) and absorbing and assimilating pollutants from their food (dietary route) (Liu et al., 2022). Trophic transfer does not necessarily mean that the prey species must have previously ingested the specific substance (Watts et al., 2014), for instance, pollutants can adhere to surfaces, exposing organisms to the direct contact. Several studies, including those by Staniszewska et al. (2015) and Azizullah et al. (2022), have underscored BPA's prominence as the primary bioaccumulated compound in phytoplankton. Consequently, the initial stage of biomagnification involves the accumulation of hydrophobic organic contaminants in algae, leading to an elevated concentration of pollutants in the food chain (Guo et al., 2017). Similar findings to ours were shown by Guo et al. (2017) for rotifer and by Magnusson et al. (2007) for copepods, demonstrating that bioaccumulation factors were more pronounced in the dietary route compared to the waterborne route. Therefore, although the current study did not specifically quantify bioaccumulation or biomagnification of BPA in zooplankton, it illustrated the harmful effect attributed to the BPA content in the food.

Secondly, in opposition to our second hypothesis, WC had a stimulatory effect on the GR of *D. magna* (measured as effect size) at low concentrations of BPA, but this effect was reversed at high concentrations of BPA. By contrast, WF had a detrimental effect on the GR of *D. magna* across the entire BPA-Food gradient (effect size). The stimulatory response suggests that WC enhances the metabolism *D. magna* and improves its tolerance to the second stressor, BPA-Food, at low levels (Jackson et al., 2016). The persistently negative effect of WF on the GR of *D. magna* along the BPA-Food gradient could be attributed to the high

energy demands of fluctuating environments (Williams et al., 2012). Energy costs incurred during the warming phase of a daily cycle may have exceeded the energetic savings during the cooling phase (Williams et al., 2012), especially for ectotherm organisms, where temperature significantly influences physiology, fecundity and body size (Tattersall et al., 2012). Additionally, organisms in highly fluctuating environments could potentially be more susceptible to additional stressors, such as pollutants, due to greater energy demand and physiological trade-offs (Willming et al., 2013; López-Valcárcel et al., 2023), leading to synergistic negative responses. In this regard, it is noticeable that BPA-assimilated threshold for WF ($\sim 100 \mu\text{g L}^{-1}$, Fig. 7), was slightly lower than that for WC ($150 \mu\text{g L}^{-1}$), suggesting that the higher metabolic costs for *D. magna* associated with fluctuating relative to constant temperatures make the animals more sensitive to negative effects of BPA-assimilated by algae. Moreover, a threshold for BPA-assimilated by algae indicated the maximum BPA value below which both warming temperature regimes showed positive effects on the GR, which vanished above the threshold, resulting in interactive effect between WC or WF and BPA assimilated by algae on the GR of *D. magna*.

Considering the daily temperature fluctuations in aquatic natural systems, experiments involving varying temperature, such as those here investigated, offer a more realistic approach for investigating thermal response in organisms (e.g. Bauerfeind and Fischer, 2014; Colinet et al., 2015; Morón Lugo et al., 2020). These findings gain significance in the context of climate change scenarios, where freshwater biota is expected to be specially impacted (LeRoy Poff et al., 2002; Woodward et al., 2016).

In cladocerans, BPA interferes with the moulting hormones (ecdysteroid), which play a central role in the onset of moulting, metamorphosis, and reproduction in arthropods (LeBlanc, 2007). Consistent with this, the results obtained highlight that even minor concentrations of BPA in food not only impact the GR of *D. magna* but also have a significant influence on their moulting capability. Under both temperature scenarios (WC and WF), moulting capacity increased at low BPA concentrations but decreased at higher BPA concentrations, irrespectively of the temperature regime. These results are also consistent with the temperature effect on *D. magna*'s GR. Moreover, our findings are in line with Li et al. (2018) and Qian et al. (2022), who, using BPA concentrations comparable to ours (i.e. $20 \mu\text{g L}^{-1}$ and $100 \mu\text{g L}^{-1}$, respectively), reported a delay in time of the first brood and a decline or inhibition in moulting frequency. Other researchers have also described adverse effects on reproduction and moulting in *D. magna*. It is essential to note that, as previously mentioned, the concentrations they used were up to 10-fold higher (Mu et al., 2005: $5\text{--}10 \text{ mg L}^{-1}$; Jemec et al., 2012: 3.45 mg L^{-1} ; Jeong et al., 2013: 6.67 mg L^{-1}).

Although not directly tied to spawning ability, moulting frequency is a fundamental physiological process in the life cycle of *D. magna*, necessary for body growth and reproduction (Brennan et al., 2006). For example, several authors have documented that species sacrifice reproduction for other biological functions in response to stress (Mensah et al., 2012; Sokolova et al., 2012) or the number of non-viable offspring increases (Religia et al., 2019), establishing a positive association between moulting and spawning times (Dai et al., 2016). Consistent with these observations, we found a positive influence of temperature on reproduction, as it enhanced the proportion of gravid females, aligning with the common observation that higher temperatures accelerate physiological processes in ectotherms (e.g. Heugens et al., 2006). However, the presence of BPA in the diet led to a reduction of over 50% in gravid females compared to organisms fed algae without BPA. Once again, this underscores that positive effects of warming temperature are offset in the presence of the primary stressor, which, in our case, is BPA in the food. Consequently, our findings reinforce the conclusions of earlier studies (e.g. McKee et al., 2002) that stressors play a crucial role as they can impact body size and various life history parameters, contributing to ecological consequences within communities.

5. Conclusion and implications

This study, by mimicking environmental BPA concentrations and those commonly used in laboratory experiments, proved that the BPA-assimilated by algae (*Scenedesmus* sp.) and transferred to *D. magna* through food, exerts pronounced detrimental effects on their growth rate, moulting ability, and reproduction. In addition, these effects are modulated by temperature, resulting in a positive impact of BPA food on the GR of *D. magna* under a warming-constant scenario at lower concentrations, but turning negative under warming-fluctuating conditions. Thus, our discovery regarding the susceptibility of *D. magna* to BPA transmitted through food underscores the significance of the environmental context in ecotoxicological assessments.

In the current scenario of the global climate crisis, which seems to be worsening (Ondrasek and Rengel, 2021), our findings gain relevance as they quantify the extend and impact of harmful BPA transmitted through food. Furthermore, our study establishes thresholds for BPA affecting *Daphnia* growth under projected future conditions of warming and fluctuating temperatures. Considering the key role of this consumer herbivore in carbon flux within aquatic ecosystems, our findings hold significance for comprehending the toxic impacts of BPA on carbon flux, along with implications for both environmental and human health. Future research is crucial for comprehensively evaluating the impact and effects of novel BPA analogues on aquatic biota. Specifically, these investigations should concentrate, as illustrated in this study, on elucidating how contaminants affect key species and the resultant implications within freshwater food webs.

CRedit authorship contribution statement

M. Fernanda Alvarez: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Manuel Villar-Argaiz:** Writing – review & editing, Visualization, Investigation, Conceptualization. **Fernando Vela Soria:** Methodology. **Alejandra Fernández Zambrano:** Methodology. **J. Manuel Medina-Sánchez:** Writing – review & editing, Visualization, Project administration, Investigation, Funding acquisition, Conceptualization. **Presentación Carrillo:** Writing – review & editing, Visualization, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envpol.2024.124186>.

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