











LETTER

A common temperature dependence of nutritional demands in ectotherms

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Abstract

In light of ongoing climate change, it is increasingly important to know how nutritional requirements of ectotherms are affected by changing temperatures. Here, we analyse the wide thermal response of phosphorus (P) requirements via elemental gross growth efficiencies of Carbon (C) and P, and the Threshold Elemental Ratios in different aquatic invertebrate ectotherms: the freshwater model species *Daphnia magna*, the marine copepod *Acartia tonsa*, the marine heterotrophic dinoflagellate *Oxyrrhis marina*, and larvae of two populations of the marine crab *Carcinus maenas*. We show that they all share a non-linear cubic thermal response of nutrient requirements. Phosphorus requirements decrease from low to intermediate temperatures, increase at higher temperatures and decrease again when temperature is excessive. This common thermal response of nutrient requirements is of great importance if we aim to understand or even predict how ectotherm communities will react to global warming and nutrient-driven eutrophication.

KEYWORDS

carbon, ecological stoichiometry, gross growth efficiency, growth, metabolism, nutrients, phosphorus, respiration, thermal gradient, threshold elemental ratio

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INTRODUCTION

Temperature is among the most influential determinants of fitness in ectotherms, as it directly drives their metabolism (Clissold & Simpson, 2015; Cross et al., 2015). Within biologically relevant ranges below the optimum temperature, ectotherm metabolic rates scale exponentially with temperature. Hence, even a small increase in environmental temperature may lead to large changes in performance (Brown et al., 2004; Gillooly et al., 2001). Furthermore, to ensure the achievement of the Darwinian functions of survival and reproduction, all consumers must obtain a diet containing the appropriate balance of biochemical nutrients (Simpson & Raubenheimer, 2012) including essential fatty acids, amino acids and vitamins. On a more basic level, specific chemical elements, such as nitrogen (N) and phosphorus (P), are also essential components of the food (Sternler & Elser, 2002). Given the overriding importance of temperature for metabolic rates of ectotherms, understanding the interactions of temperature and nutritional demands is critical (Cross et al., 2015). The most straightforward way to assess temperature–food quality interactions is to investigate temperature effects on the Threshold Elemental Ratio (TER) (Frost et al., 2006; Sternler, 1997; Urabe & Watanabe, 1992). The $TER_{C:X}$ is the carbon:nutrient (C:X) ratio in the food that matches the current physiological requirements for metabolism and growth of the consumer, with neither C nor X being limiting or in excess. The TER is a quantitative tool that integrates multiple responses of organism biochemistry and physiology. A low $TER_{C:X}$ indicates higher needs for the nutrient X relative to C, while a higher $TER_{C:X}$ indicates the opposite. Cross et al. (2015) noted that there were few studies on how temperature affects the TER and made a strong case to measure the $TER_{C:X}$ at different temperatures.

The integration of two theoretical frameworks may lead to a general theory to understand how energy and nutrient availability act in combination: the metabolic theory of ecology (MTE) from Brown et al. (2004), which focuses on the importance of individual energetics; and ecological stoichiometry theory (EST) that focuses on the importance of element availability (Sternler & Elser, 2002). In the frame of MTE, a positive relation of an organism's C requirements with temperature is expected as a consequence of the over-proportional increase in respiration rates with temperature, resulting in an increasing $TER_{C:X}$ with temperature as seen by Boersma et al. (2016) and Malzahn et al. (2010). However, assuming that respiration and feeding rates scale equally with temperature (same Q_{10}) and that invertebrates facing nutrient limitation at increasing temperatures might use their excess C to meet the increased demands for energy without the need for extra dietary C, Anderson et al. (2017) modelled a constant $TER_{C:N}$ with temperature. On the other hand, growth has a lower C:nutrient

than metabolism so a decreasing $TER_{C:P}$ with temperature is expected if growth scales faster (larger Q_{10}) than respiration.

Studies on stoichiometric impacts of temperature are, unfortunately, rather equivocal, with reports of increasing, decreasing or constant TER with increasing temperature (Anderson et al., 2017; Boersma et al., 2016; Malzahn et al., 2016; Persson et al., 2011; Ruiz et al., 2020; Wojewodziec et al., 2011). The most parsimonious explanation for these findings is that the response of the nutritional demands to temperature is not monotonic and that most studies conducted so far have not covered a sufficiently broad temperature range. Indeed, based on the parametrisation of $TER_{C:P}$ model from Frost et al. (2006) with literature data on the temperature dependencies of all parameters in the model and with experimental data on growth-based $TER_{C:P}$, Ruiz et al. (2020) predicted a U-shaped response of the $TER_{C:P}$ with temperature. Hence, the question remains whether there is a common response of ectotherm nutrient requirements to changing temperatures that would help in making predictions about secondary production responses to global change. Alternatively, the diversity of findings to date may reflect true idiosyncrasies in temperature responses among taxa, consequently preventing general overarching predictions.

In this study, we aim to shed light on the interactions between macronutrient requirements of ectotherms and temperature. We experimentally determined the response of the $TER_{C:P}$ to temperature for different aquatic invertebrates. We used two different clones of the freshwater cladoceran *Daphnia magna* with different thermal histories to determine the growth-based $TER_{C:P}$. Further, we characterised the thermal response of fundamental parameters of the bioenergetics $TER_{C:P}$ model (respiration, ingestion, growth, gross growth efficiencies of C and P, and body C:P) (Doi et al., 2010; Frost et al., 2006; Halvorson et al., 2015) across ecologically relevant temperature ranges, using one clone of *D. magna* (same as growth-based TER), the marine copepod *Acartia tonsa*, the marine heterotrophic dinoflagellate *Oxyrrhis marina*, and larvae of two populations of the marine crab *Carcinus maenas*.

Thermal performance curves of respiration and ingestion vary with increasing temperature, usually displaying an ascending phase, a peak, which indicates the thermal optimum, and a descending phase of metabolic inhibition (Shah et al., 2021). Growth rate increases with increasing temperature and is in part responsible for the increase in ingestion, due to the extra demands for substrates (Hayes et al., 2015). Body C:P is expected to increase with temperature (Balseiro et al., 2021; Woods et al., 2003), while for GGEs decreasing, increasing and constant thermal responses were reported (Doi et al., 2010; Hagerty et al., 2014; Smith et al., 2021; Ye et al., 2019; Zheng et al., 2019). Based on these hypothesised mechanisms, we predict that ectotherm nutrient

requirements change with temperature in a nonlinear fashion, as a response to nonlinear thermal reaction norms of metabolism and growth.

MATERIALS AND METHODS

First, we determined the thermal response of the $TER_{C:P}$ from growth rates as a function of temperature and food C:P (growth-based $TER_{C:P}$) for two clones of *Daphnia magna*. The $TER_{C:P}$ is obtained from the diet C:P, which maximises growth, at different temperatures. Secondly, to explore the mechanisms underlying the thermal response of the $TER_{C:P}$, we determined the thermal response of body C and P contents and ingestion (IR), respiration (RR) and growth (GR) rates, the gross growth efficiency of C and P (GGE_C and GGE_P) and the $TER_{C:P}$ bioenergetic model proposed by (Doi et al., 2010; Frost et al., 2006) following Halvorson et al. (2015). This was done for *Acartia tonsa*, *Oxyrrhis marina* and larvae of two different populations of *Carcinus maenas*, and one clone of *D. magna* (same used in the growth-based $TER_{C:P}$). With this second set of experiments, we obtained information on how nutrient requirements of the studied organisms change with temperature, as well as the thermal response of all underlying variables that determine the TER (model details in Appendix S1).

Growth-based $TER_{C:P}$ as a function of temperature

We determined the diet C:P, which maximises growth ($TER_{C:P}$) at different temperatures for two clones of *D. magna*. These two clones differ in their thermal histories. Clone US was maintained in the laboratory at 24–25°C, and Clone AR at 20°C, both for at least 3 years prior to experiments (see below for details). The thermal optimum for *D. magna* ranges between 16 and 22°C (Bruijning et al., 2018).

Culturing conditions

The first experiment was carried out at Arizona State University, USA, with a clone of *D. magna* (Clone US) that was maintained in the laboratory in COMBO media (Kilham et al., 1998) on a diet of the green alga *Scenedesmus acutus* (C:P~120) at room temperature (24–25°C). The experiment was carried out at 18, 23 and 28°C in a food quality gradient consisting of food with five C:P ratios ranging from 51 to 816. The second experiment was carried out at Universidad Nacional del Comahue, Argentina, with a clone of *D. magna* (Clone AR) that had been maintained in the laboratory in COMBO media (Kilham et al., 1998) on a diet of the green algae *Chlamydomonas reinhardtii* (C:P~150) at 20°C. We used

15, 20 and 24°C as temperatures and a C:P gradient ranging from 40 to 746.

Experimental design

Both experiments lasted 3 days to avoid the confounding effect of shifts in allocation between growth and ovary development of *Daphnia* reaching maturity (Acharya et al., 2004). To exclude the influence of indirect effects of P limitation on the biochemistry of the algae, the gradients in food quality (C:P) were created with a short-term P-spiking technique following Rothhaupt (1995) and Plath and Boersma (2001) (Details in Appendix S2).

For both experiments, we placed one 24-h-old *D. magna* in a 30ml beaker with 11 replicates in a factorial design of 3 temperatures and 5 food qualities ($n = 165$). Food and media were replaced daily at a concentration of 1.5 mgCL⁻¹. To determine growth rate, the area of each animal was measured by taking lateral images and then processing the image via Image-Pro Plus (Media Cybernetics) software. These measurements were converted to dry weight based on our own area–weight regressions obtained from our *D. magna* cultures at different food qualities. We determined the growth rate of each individual as the difference in the natural logarithm of the dry weight at the end and the beginning of the experiment divided by the time in days. In some cases, one or two replicates were missing at the end of the experiment due to mortality during the daily handling of the animals.

Data analyses

The shape of the $TER_{C:P}$ thermal reaction norm was obtained following Ruiz et al. (2020). For each temperature level separately, the following modified Gaussian function was fitted to the relationship between individual growth rate versus the food C:P from which $TER_{C:P}$ estimates were derived:

$$GR = a + b * e^{-E * \frac{C:P - c}{d^2}} \quad (1)$$

where C:P is the food C:P ratio, a is the minimum growth rate, b is the height of the curve, c is the estimated $TER_{C:P}$ (i.e., curve's maximum), d is the curve breadth and E is a scaling parameter. All the parameters were estimated by nonlinear least squares regression (Baty et al., 2015). The confidence intervals around the $TER_{C:P}$ were estimated by nonparametric bootstrapping (Efron & Tibshirani, 1986). At each temperature, the dataset was resampled 1000 times and the nonlinear regression procedure and $TER_{C:P}$ estimations were reiterated. This was used to calculate the mean $TER_{C:P}$ and the 95% confidence intervals ($CI_{95\%}$) for each temperature. A

significant difference between $TER_{C:P}$ estimates at each temperature was inferred in the absence of overlap between their $CI_{95\%}$.

Thermal response of the bioenergetic $TER_{C:P}$ and underlying variables

Culturing conditions

Experiments were carried out at the Universidad Nacional del Comahue, Argentina (*D. magna* AR) and the Biologische Anstalt Helgoland (BAH), AWI, Helgoland, Germany, for the rest of the species. *D. magna* (AR) is the same clone as the growth-based $TER_{C:P}$. *O. marina* was obtained from the Göttingen culture collection (Strain B21.89), and the stock culture used to inoculate the experimental containers was grown in batch cultures at 18°C in the dark. Eggs of *A. tonsa* were obtained from a permanent laboratory culture at 18°C and incubated in filtered seawater for hatching, and only those hatched between 24–36 h of incubation were used. Berried females of *C. maenas* were collected manually at the intertidal area of the bay of Cadiz (Spain) and Helgoland (Germany) during the reproductive periods. Suitable temperature for embryonic development and larval release occurs in February–March (15.3–16°C) for the Cadiz population, and in May–July (9–15°C) for the Helgoland population. Animals were transported to the BAH in individual containers with seawater and constant temperature (15.7 and 12.5°C for Cadiz and Helgoland, respectively). To ensure a successful embryonic development, and to reflect the temperature of the natural habitat at the time of hatching in summer, females were maintained in individual aquaria where temperature was gradually increased (0.2°C per day) until 18°C, when hatching occurred. We used four hatches from different females from the Cadiz population and three from Helgoland to account for maternal effects on the results (Torres et al., 2020), and each of them was considered a replicate.

Experimental design

24-h-old *D. magna* (AR) were placed in beakers with COMBO and food (*C. reinhardtii*) ad libitum. Individuals of *O. marina*, or recently hatched *A. tonsa* (nauplii) and *C. maenas* (Zoea I) were placed in beakers with filtered seawater (0.2 µm) and food ad libitum. *A. tonsa* and *O. marina* were fed *Rhodomonas salina*, and *C. maenas* was fed with *Artemia salina*. *D. magna* (15 and 24°C), *A. tonsa* and *C. maenas* (12–24°C) were distributed in temperature-controlled rooms, and *O. marina* beakers were placed in a gradient temperature table (15.2–22.8°C) following Malzahn et al. (2016).

Media and food were replaced daily. The length of the experiment varied according to each species (Details in Appendix S3, Table S1).

Carbon and phosphorus analyses

At the beginning and the end of the experiments, we determined C and P contents for individuals of *D. magna*, *A. tonsa* and *C. maenas*. Carbon and P contents per beaker of *O. marina*, *C. reinhardtii* and *R. salina* were measured by filtering a known amount through acid-washed pre-combusted (450°C, 2 h) Whatman GF/F filters. Analyses for *D. magna*, *A. tonsa* and *A. salina* were carried out by placing a known number of individuals on GF/F filters and for *C. maenas* by placing individuals directly into pre-weighed tin capsules for C analysis or in 1.5 ml Eppendorf tubes for P analysis, following by re-weighing before analysis. C was analysed with a Vario MICRO cube CHNS analyser (Elementar Analysensysteme), and P as orthophosphate after acidic oxidative hydrolysis (Grasshoff et al., 2009). Using these data, we calculated initial and final body C:P ratios and growth rate in terms of C and P for each species (*GR*, see calculations).

Ingestion (IR) and respiration (RR)

At the end of the growth periods, we determined ingestion rates in terms of C and P and respiration rates for all the organisms in the dark. Ingestion rates of *D. magna* were obtained with the fluorescent microspheres method following DeMott (1986); Wiedner and Vareschi (1995); Laspoumaderes et al. (2017). Ingestion rates of the other species were determined through the difference in final food concentration versus a control for *O. marina* and *A. tonsa*, or versus initial concentration for *C. maenas* (details in Appendix S3b and S3, Table S2).

Respiration rates were assessed as oxygen consumption over time in glass vials with the organisms, media without food, in the dark, stoppered to ensure that no air bubbles were present, in temperature-controlled rooms set to the experimental temperature. Vials without organisms ($n = 5-6$) were used as controls to account for microbial oxygen consumption. Oxygen consumption was determined by linear regression of O_2 concentration against time, standardised to µgC (details in Appendix S3c and S3, Table S3).

Calculations

We determined the $TER_{C:P}$ as a function of temperature for *D. magna* (AR), *A. tonsa*, *O. marina* and *C. maenas* using the model of Frost et al. (2006) modified by Doi et al. (2010) and further analysed by Halvorson et al. (2015) (Equation 2):

$$TER_{C:P} = \frac{GGE_P}{GGE_C} \times \frac{Q_C}{Q_P} \quad (2)$$

where Q_C and Q_P are the final body C and P contents (for alternatives see Appendix S1), GGE_P and GGE_C are the gross growth efficiencies of P and C calculated following Doi et al. (2010) as the ratio of the growth rate of P or C to the ingestion rate of P or C (for GGE_P and GGE_C , respectively):

$$GGE = \frac{GR}{IR} \quad (3)$$

where GR is the amount of C or P fixed as new biomass in a certain period, it is calculated as the difference in C or P content (per individual for *D. magna*, *A. tonsa* and *C. maenas*, and per beaker for *O. marina*) at the end and the beginning of the experiment over time in days, and IR is the ingestion rate in terms of C or P in the same period.

We calculated the Q_{10} of RR , IR and GR in the thermal gradient with the formula:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10/T_2-T_1}$$

where R_1 and R_2 are the specific rates at temperatures 1 and 2, respectively (T_1 and T_2). When the $TER_{C:P}$ was non-linear, we calculated the Q_{10} separately for the increasing and decreasing thermal range. We compared the Q_{10} of respiration with the Q_{10} of ingestion and growth for each thermal range.

Data analyses

One-way analysis of variance (ANOVA) was performed to compare the organisms' C:P ratios, respiration, growth and ingestion rates, GGE and $TER_{C:P}$ values with temperature as a factor, followed by Holm-Sidak post hoc tests. When assumptions were not met, Kruskal-Wallis ANOVA on ranks was used. The temperature where the $TER_{C:P}$ is the highest (Max $TER_{C:P}$ temperature) and its $CI_{95\%}$ for *A. tonsa*, *O. marina* and *C. maenas* were obtained through nonlinear regression fit of the thermal response of the $TER_{C:P}$ to a Gaussian function, with the R package nlstools (Baty et al., 2015). The Q_{10} were compared with t -tests. Analyses were performed using the software R v.4.1.2 (R-Core-Team, 2021).

RESULTS

Growth-based $TER_{C:P}$ as a function of temperature

Growth rates of both clones of *D. magna* showed a hump-shaped response to the food C:P gradient and fitted to the Gaussian equation (Equation 1) at all temperatures

(Figure 1a,b), except for *D. magna* (US) at 15°C (lowest temperature), which showed a nearly flat response of growth rates to changing food quality (Figure 1a) (See Appendix S4a model fitting). The $TER_{C:P}$ at each temperature (maximum of the gaussian function, except for *D. magna* (US) at 15°C), showed a hump-shaped relation with temperature. The maximum $TER_{C:P}$ was found at intermediate temperatures for both clones (Figure 1c,d), with decreasing $TER_{C:P}$ at low and high temperatures (Figure 1c,d).

Thermal response of the bioenergetic $TER_{C:P}$ and underlying variables

Ingestion, respiration and growth rates in the thermal gradient

Ingestion and respiration rates showed the same response to temperature within species but were not consistent between them (Figure 2). The change in ingestion rates in *D. magna* (AR) with temperature was not significant; however, respiration increased (Figure 2a,b). Ingestion and respiration rates showed a hump-shaped response to temperature for *A. tonsa* and *O. marina*, with maximum values in the range of 18–21°C for *A. tonsa*, and at 18°C for *O. marina* (Figure 2d,e,j,k). In contrast, both populations of *C. maenas* presented a consistent increase in ingestion and respiration (Figure 2g,h,m,n). Growth rates had an increasing trend in the thermal gradient for all species (Figure 2c,f,i,l,o). However, growth rates of both populations of *C. maenas* seemed to reach a maximum growth at around 21°C (Figure 2i,o).

Body C:P in the thermal gradient

Body C:P of *D. magna* was higher at 24°C than at 15°C (Figure 3a). C:P of *A. tonsa*, *O. marina* and *C. maenas* (Cadiz (C)) had a U-shaped response to temperature, with minimum values at intermediate temperatures (around 18°C) (Figure 3b–d). C:P ratios of *C. maenas* (Helgoland [H]) showed the same U-shaped response to temperature but also had a second minimum in the highest temperatures resulting in an “inverse N-response” of body C:P to temperature (Figure 3e).

Gross growth efficiency of C and P (GGE_C and GGE_P) in the thermal gradient

The thermal response of gross growth efficiency of carbon presented some differences between species (Figure 3f–j). GGE_C in *A. tonsa* increased at the highest temperature (Figure 3g), had a U-shaped response to temperature in *O. marina* (Figure 3h), and had no variation with temperature for both *C. maenas* populations

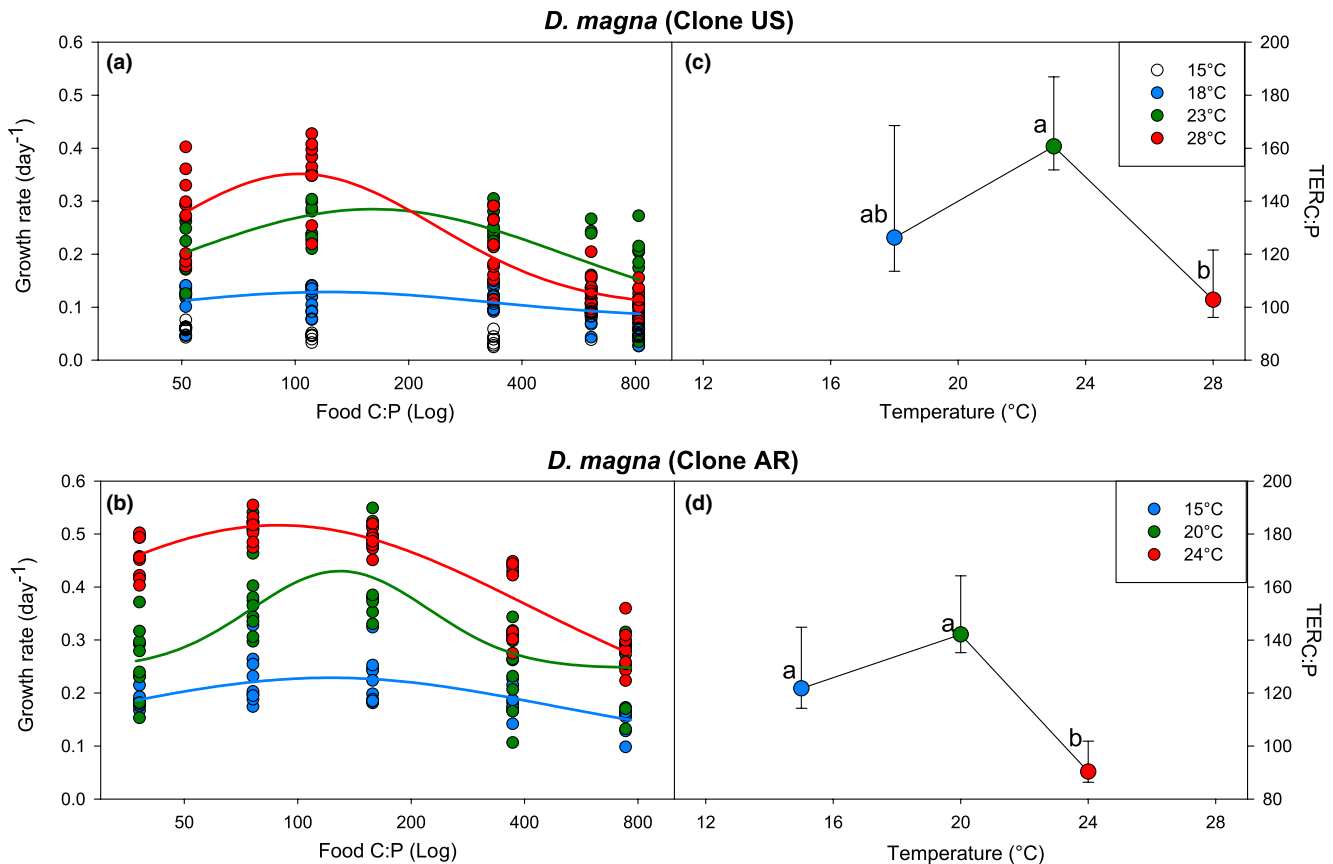


FIGURE 1 (a) and (b) Growth rate as a function of food C:P ratio in the thermal gradient for clone US (a) and clone AR (b) of *Daphnia magna*. Dots are individual data, and the lines are the best fit to the Gaussian Function (Equation 1) estimated by nonlinear least squares regression, the maximum of the gaussian function is the C:P threshold elemental ratio (TER_{C:P}). (c) and (d) TER_{C:P} as a function of temperature and the 95% confidence intervals (CI_{95%}) estimated by nonparametric bootstrapping ($n = 1000$) for clone US and clone AR, respectively. Lower-case letters inside the graphs indicate homogeneous groups according to overlapping CI_{95%}. Lines and dot colours represent different temperatures (see reference in figure)

and *D. magna* (Figure 3f, i, j). On the other hand, GGE_P showed larger responses to temperature with patterns that differed among the study taxa (Figure 3f–j).

Bioenergetic TER_{C:P}

For *D. magna*, the TER_{C:P} was higher at 15°C than at 24°C. This was consistent with the growth-based and bioenergetic TER_{C:P} calculated with final and initial body C:P (Figure 1d and 4a, and Appendix S5). However, using initial body C:P, the TER_{C:P} was closer to growth-based TER_{C:P} than using final body C:P. As only two temperatures were tested for *D. magna* with the bioenergetic model, we do not know the shape of the response in the complete thermal gradient. For the other species, the bioenergetic TER_{C:P} was determined for a broad temperature range and we obtained a hump-shaped response of the TER_{C:P} to temperature for *A. tonsa*, *O. marina* and *C. maenas* (C) (Figure 4b–d), with a maximum TER_{C:P} (MaxTER_{C:P}) at intermediate temperatures. This MaxTER_{C:P} is indicative of the organism's lowest P-requirements. The unimodal

shape of the TER_{C:P} indicates that at both lower and higher temperatures animals need food with higher P content relative to C to grow maximally. In the case of *C. maenas* (H), we obtained an N-shaped response of the TER_{C:P} as a function of temperature (Figure 4e). The lower temperatures of the gradient (12–18°C) resulted in a hump-shaped response for this population similar to the other taxa, while the warmer temperatures (18–24°C) formed a U-shaped thermal response of the TER_{C:P} (Figure 4e).

Q_{10} for respiration, ingestion and growth

The Q_{10} values for respiration, ingestion and growth showed different patterns in the different areas of the TER_{C:P} (increasing and decreasing arms) for all species (Table 1). The Q_{10} of respiration was higher than the Q_{10} of ingestion and growth in the increasing arm of the TER_{C:P} for *O. marina* and the opposite pattern was observed for the decreasing arm (Table 1). For the other species, we observed that Q_{10} of respiration was higher than Q_{10} of ingestion or growth in the increasing arm, and that the Q_{10} of

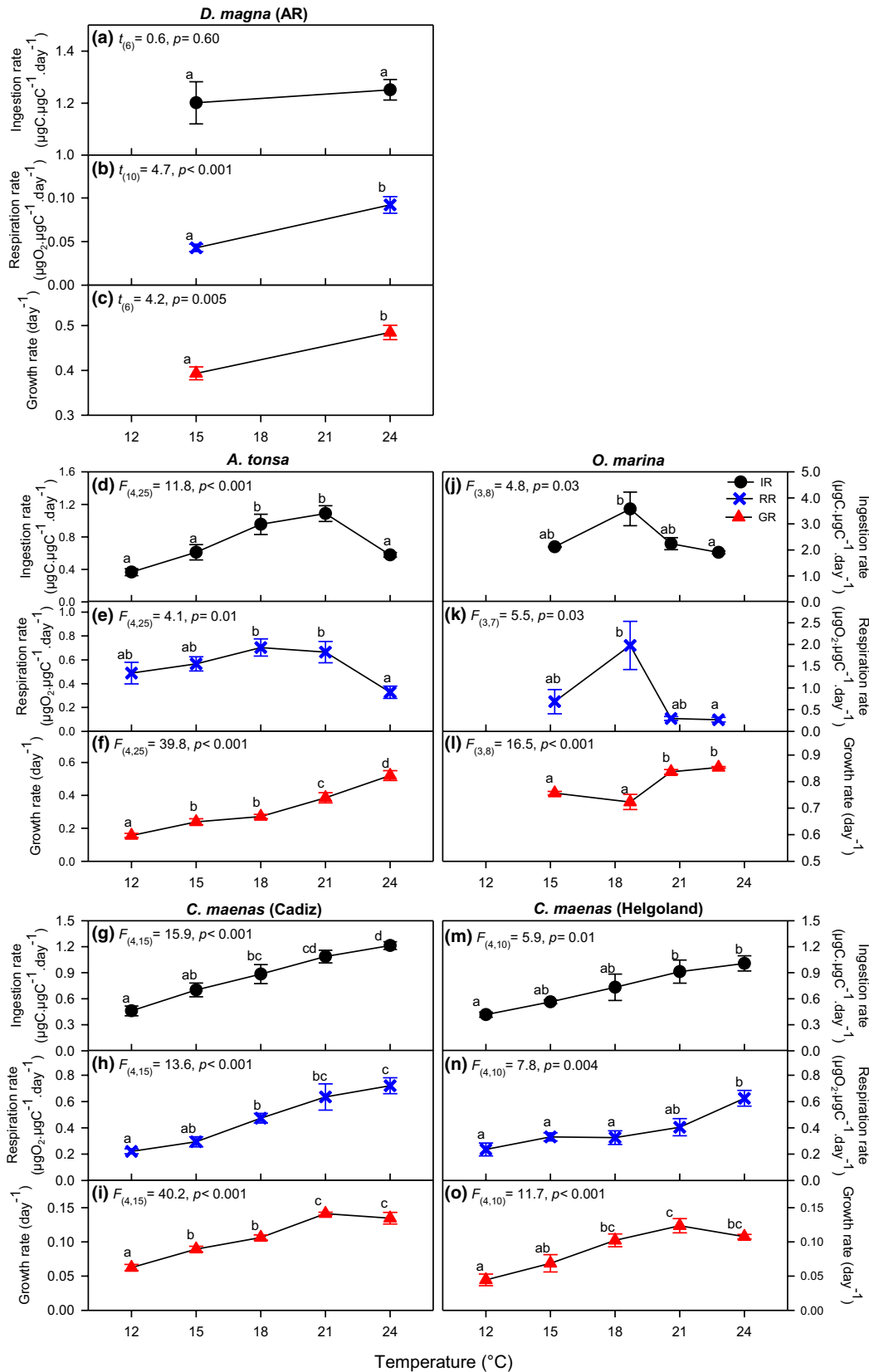


FIGURE 2 Thermal response of ingestion rate (a, d, g, j, m), respiration rate (b, e, h, k, n) and growth rate (c, f, i, l, o), for *Daphnia magna* (AR) (a–c), *Acartia tonsa* (d–f), *Carcinus maenas* (Cadiz) (g–i), *Oxyrrhis marina* (j–l) and *C. maenas* (Helgoland) (m–o). Symbols are mean values and bars SE. In some cases, the error bars are not visible, because they are smaller than the symbols. Lower-case letters inside the graphs indicate homogeneous groups according to the post hoc Holm-Šidák multiple comparison test results

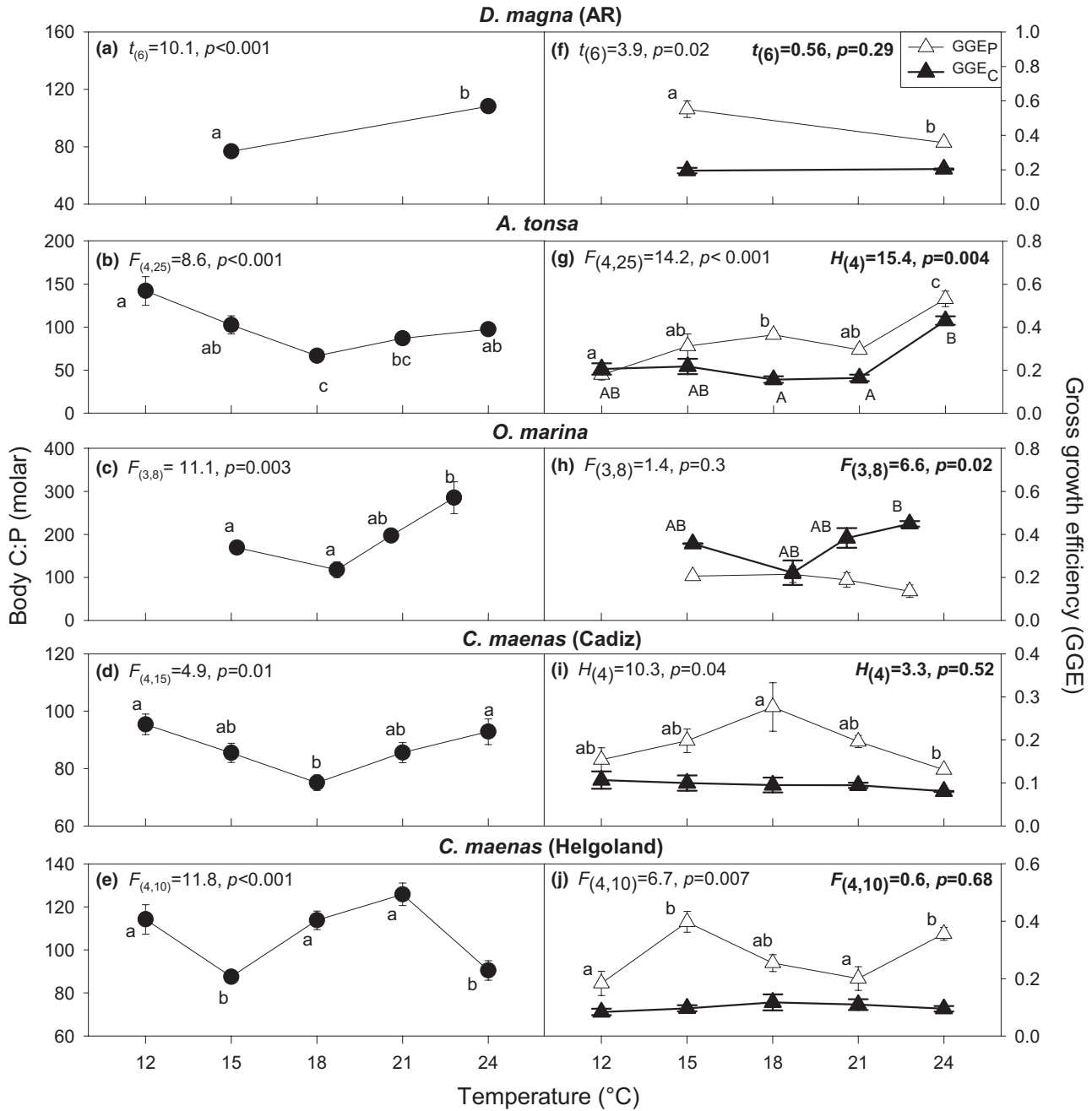


FIGURE 3 Thermal response of the body C:P ratios (a–e) and gross growth efficiency (GGE) of C and P (f–j) for all studied taxa. Dots are for body C:P, filled triangles are for GGE_C and empty triangles for GGE_P , symbols and bars are mean values and SE. In some cases, the error bars are not visible, because they are smaller than the symbols. Lower-case letters inside the graphs indicate homogeneous groups according to the t -test (a and f), post hoc Holm-Šidák multiple comparison test results, or Kruskal-Wallis ANOVA on ranks (i) for body C:P, and GGE_P and upper-case letters are for GGE_C .

respiration was lower than the Q_{10} of ingestion or growth in the decreasing arm of the $TER_{C:P}$ (Table 1).

DISCUSSION

Considering all the studied taxa, we observed a common thermal response in their interactive temperature-nutrient requirements with a hump-shaped $TER_{C:P}$.

These results were obtained applying two different methods, the growth-based and the bioenergetic $TER_{C:P}$. Somatic growth can be constrained by the reduction in metabolism due to low temperatures (Brown et al., 2004), and also as a consequence of P-limitation or excess when food contains too high or low C:P ratios (Plath & Boersma, 2001). When we analysed growth of *Daphnia* in the food C:P and temperature gradient, we found support for the knife-edge

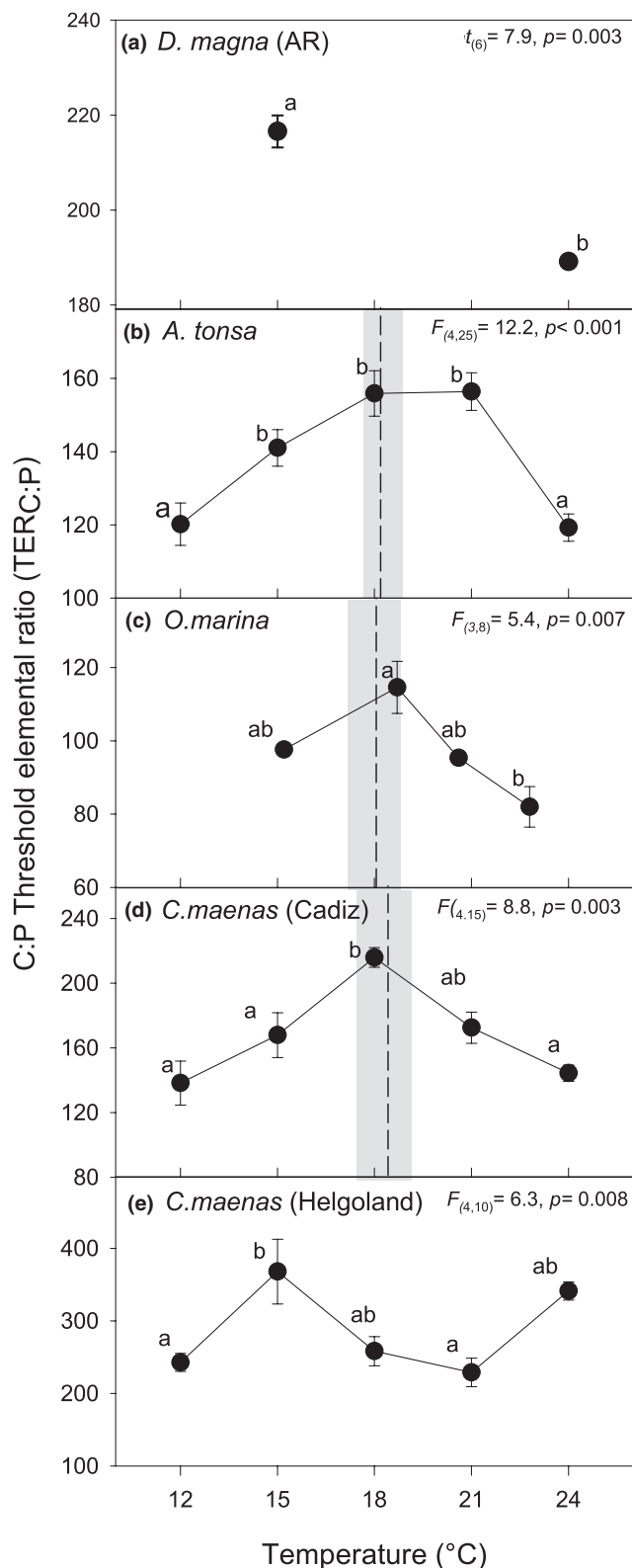


FIGURE 4 C:P Threshold Elemental Ratio (TER_{C:P}) as a function of temperature for (a) *Daphnia magna* (AR), (b) *Acartia tonsa*, (c) *Oxyrrhis marina*, (d) *Carcinus maenas* Cadiz and (e) *C. maenas* Helgoland. Symbols are mean values and bars SE. In some cases, the error bars are not visible, because they are smaller than the symbols. In (b–d), dashed vertical lines represent the mean MaxTER_{C:P} temperature and the shaded areas the CI_{95%} obtained through non-linear regression fit of the thermal response of the TER_{C:P} to a Gaussian function, with the R package nlstools (Baty et al., 2015). Dots and bars are mean values and SE. Lower-case letters inside the graphs indicate homogeneous groups according to t -tests (a), or the post hoc Holm-Šidák multiple comparison test results

et al., 2011), suggesting that the constrain imposed by low temperature is stronger than that by food quality. The lack of a TER_{C:P} identification in the cold *D. magna* treatment implies poor energy availability for somatic and gonadic growth, which agrees with identified thermal optimal range for growth (from 16 to 22°C (Bruijning et al., 2018)). The bioenergetic TER_{C:P} for *D. magna* tested at two different temperatures, showed the same thermal pattern as the growth-based TER at the same two temperatures, but different absolute values (Figure 1b and 4a, Appendix S5). Because we obtained the same pattern in the TER_{C:P} of *D. magna* (AR) with the growth-based and bioenergetic model, we determined the bioenergetic TER_{C:P} in a thermal gradient for the other species, as it provides information on the thermal reaction norms of the underlying variables driving the TER_{C:P} (Details in Appendix S1).

The observed hump-shaped TER_{C:P} indicates that P requirements are high at low temperatures, decrease when temperatures increase to intermediate values, and increase again when temperatures are higher. The low TER_{C:P} at low temperatures provides support for the “Compensatory Hypothesis” (Persson et al., 2011) which states that P requirements should be high at low temperatures to compensate for the thermal constrain on enzymatic activity. Metabolic theory predicts that the shape of the TER_{C:X} can be explained by the relation between the Q_{10} of respiration and ingestion (Anderson et al., 2017; Ruiz et al., 2020). When respiration has a lower Q_{10} than ingestion, the TER_{C:X} is expected to decrease. In agreement with the metabolic theory, Ruiz et al. (2020) found the minimum TER_{C:P} in their “U-shaped TER” at the temperature where respiration starts increasing faster than ingestion. On the other hand, metabolism has higher C:nutrient requirements than growth, so an increasing TER_{C:P} with temperature is expected if respiration scales faster than growth. We suggest that the relation between Q_{10} of respiration, ingestion and growth can contribute to explain the hump-shaped TER_{C:P}. An increasing TER_{C:P} is expected when Q_{10} of respiration is larger than Q_{10} of ingestion and/or growth; and a decreasing TER_{C:P} should be expected when Q_{10} of respiration is smaller than the Q_{10} of ingestion and/or growth. In our study, this combination was observed as predicted in the increasing arm of the TER_{C:P} of *O. marina*,

hypothesis and the metabolic theory, as growth was depressed at extreme food C:P, and at low temperature (Figure 1a,b). The flattening of the growth curves with decreasing temperature implies that the effect of food quality on growth decrease with temperature (Persson

	Variable	Increasing TER _{C:P}	Decreasing TER _{C:P}	Increasing TER _{C:P}
<i>A. tonsa</i>	RR	3.12 (1.10)	0.34 (0.10)	
	IR	6.10 (2.00) ^{ns}	0.51 (0.10) ^{ns}	
	GR	2.78 (0.26) ^{ns}	3.08 (0.42) ^{***}	
<i>O. marina</i>	RR	20.73 (2.00)	0.008 (0.006)	
	IR	4.48 (2.4) ^{**}	0.22 (0.09) [*]	
	GR	0.87 (0.10) ^{***}	1.51 (0.15) ^{***}	
<i>C. maenas</i> (C)	RR	3.63 (0.42)	2.16 (0.46)	
	IR	3.50 (0.96) ^{ns}	1.99 (0.63) ^{ns}	
	GR	2.47 (0.24) [*]	1.50 (0.16) ^{ns}	
<i>C. maenas</i> (H)	RR	3.13 (0.98)	1.22 (0.13)	6.37 (2.25)
	IR	2.46 (0.63) ^{ns}	2.26 (0.48) ^{ns}	1.56 (0.67) ^{ns}
	GR	4.35 (0.46) ^{ns}	2.87 (0.52) [*]	0.67 (0.15) [*]

Note: Superscripts indicate the results of the *t*-test of RR versus IR, and RR versus GR. ns indicates no significant differences, **p*<0.05, ***p*<0.01, ****p*<0.001.

C. maenas (C) and on the second increase of *C. maenas* (H), while for *A. tonsa* and the first increase in *C. maenas* (H) the Q_{10} of respiration did not differ for ingestion and growth. In addition, as predicted, in the decreasing arm of the TER_{C:P} of *A. tonsa*, *O. marina* and *C. maenas* (H), Q_{10} of respiration was lower than Q_{10} for ingestion and/or growth (Table 1, Appendix S4b, Table S3). The Q_{10} in *D. magna* was not included in this study as we are likely to have an optimum between the two temperatures that would lead to misleading results.

Ingestion, respiration, growth and GGEs are affected not only by temperature but also by food quality. This can lead to confounding effects of food quality on the thermal response of all underlying variables of the TER_{C:P}. Ingestion rates increase when facing imbalanced food to increase the acquisition of the limiting element (Hessen et al., 2013), respiration rates increase when food is C-rich as a pathway to dispose of excess C (Darchambeau et al., 2003), and GGEs of C and P tend to decrease when the element is non-limiting (Frost et al., 2004). In our study, food C:P was the same at all temperatures for each species but consumer nutrient requirements (TER_{C:P}) differed with temperature. Hence, the imbalance accounted for the difference in elemental composition of the food and that required by the consumer (TER_{C:P}) differed with temperature. This may affect the response of the variables driving the TER_{C:P} to temperature.

Understanding the thermal dependencies of nutrient GGEs may open the path towards integrating metabolic theory and ecological stoichiometry. In an attempt to do so, Doi et al. (2010) compiled data from the literature, but were not able to find a universal relationship between GGE_P and temperature. They concluded that it is difficult to make robust inferences due to limited number of assessments of GGE_P. We find, GGE_P to be an important driver of the TER_{C:P} in the thermal gradient for three (both *C. maenas* and

TABLE 1 Q_{10} of respiration rates (RR), ingestion rates (IR) and growth rates (GR), for all taxa in the analyses, for the increasing and decreasing arms of the TER_{C:P}

D. magna) out of five organisms in the analyses and we found that, in general, GGE_P seems to be high at the MaxTER_{C:P} temperature. We do not know whether there is a universal pattern for the thermal dependence of GGE. However, the nonlinear thermal responses of GGE_C and GGE_P result in a complex nonlinear thermal response of nutrient requirements. The humped-shaped and N-shaped thermal responses of the TER_{C:P} were a result of the relation between the GGE of P and C, while the body C:P ratio generated changes in the absolute values of the TER_{C:P} but not in the thermal shape or the response (Appendix S5).

We observed that body C:P stoichiometry changes significantly with temperature, as indicated in previous work (Balseiro et al., 2021; Kendrick & Benstead, 2013; Woods et al., 2003) but in contrast to Ruiz et al. (2020). Body C:P had a nonlinear U-shaped thermal response, with a minimum C:P located at the MaxTER_{C:P} temperature. In addition, for *C. maenas* (H) we found a second body C:P minimum at the highest temperature of the range we studied. The response of body C:P to temperature showed the opposite pattern compared to the thermal response of the TER_{C:P} (Figures 3 and 4). This pattern is expected to be stronger when C:P is more variable, as the calculation of the TER_{C:P} involves the ratio of the growth of P and C. However, differential use efficiencies of C and P will lead to deviations from this inverse relation between TER_{C:P} and body C:P, until GGE_P equals GGE_C then TER_{C:P} equals body C:P.

Our hump-shaped TER_{C:P}-temperature relationship may appear to conflict with the study of Ruiz et al. (2020), which reported a U-shaped TER_{C:P} response to temperature. In Ruiz et al. (2020), however, temperatures were mainly above the optimal ones of the studied organisms. Here, we aimed to study more ecologically relevant temperatures, so our experiments did not include high temperatures, except for *C. maenas* (H). Interestingly, when we extended the model of Ruiz

et al. (2020) to lower temperatures (below 18°C), we obtained an N-shaped TER response to temperature (See Appendix S4c). Indeed, the *C. maenas* (H) population (Figure 4d) seem to provide experimental support for the extension of the model by Ruiz et al. (2020) to lower temperatures. Based on the observed results, our working hypothesis is that the observed N-shaped $TER_{C:P}$ is likely a general pattern. We suggest that more studies exploring broad thermal ranges are needed to determine if encompassing the entire operating temperature range of a species, the hump-shaped $TER_{C:P}$ responses, that we observed here, can be combined with the U-shape found by Ruiz et al. (2020), resulting in a cubic thermal response of the $TER_{C:P}$ (See Figure 5 for our hypothesised N-shaped $TER_{C:P}$).

The $MaxTER_{C:P}$ temperature might be related to the temperature of acclimation or the normal habitat temperature of the organisms in the study. The $MaxTER_{C:P}$ temperature was higher for *D. magna* (US) than for *D. magna* (AR), whose historical temperatures were 24–25 and 20°C, respectively. The same happened for both

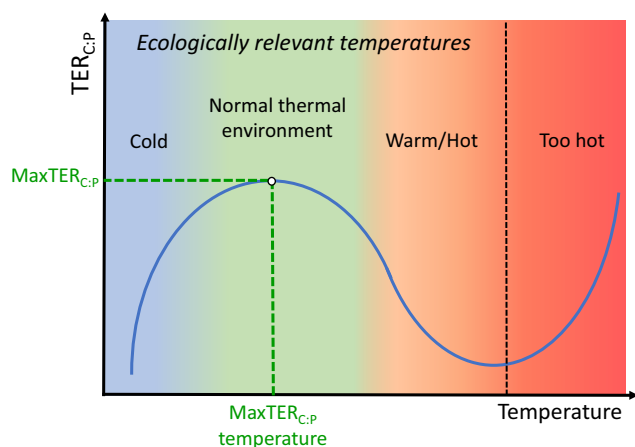


FIGURE 5 Hypothesised response of the $TER_{C:P}$ to a broad temperature range. Light blue, green and orange areas, until the vertical dashed line, represent temperatures within the ecological environment of the species (is the experimental temperature range for *A. tonsa*, *O. marina* and *C. maenas* (C)). The red area represents temperatures beyond the thermal optimum (Pörtner, 2012; Pörtner & Farrell, 2008) that might be experienced by the species only in rare conditions (we suggest that this was the case of *C. maenas* (H) in the highest temperature in our experiments). In this hypothesised concept, the increasing demands of C relative to P when temperatures increase from cold (light blue) to intermediate (middle green) are the result of increasing respiration rates and P use efficiency, until the $MaxTER_{C:P}$ is reached. When temperatures increase above the normal thermal environment of the organism (from green to orange area), the increasing demands of P relative to C are the result of the decrease in P use efficiency, the higher Q_{10} of growth and ingestion in relation to respiration, and might prevent an excessive increase in metabolism that can result from the combination of low P diets (Ruiz et al., 2018; Ruiz et al., 2020) and increased temperatures. The increase in C demands relative to P when temperature is excessive may reflect the physiological stress that amplifies C-demands for respiratory and catabolic processes (Schmitz, 2013) with higher Q_{10} of respiration than ingestion and growth

populations of *C. maenas*. The $MaxTER_{C:P}$ temperature was around 18°C for the population from Cadiz and around 15°C for the colder Helgoland population, while for *O. marina* and *A. tonsa*, the $MaxTER_{C:P}$ temperature was around 18°C, the temperatures in the laboratory cultures. So, we propose that the $MaxTER_{C:P}$ observed for all species at intermediate temperatures might reflect lower P requirements at temperatures that are close to the species' thermal environment in nature (Figure 5). This response would optimise P metabolism, given that this element is often limiting in aquatic environments.

Human activities have altered, and will continue to alter, biogeochemical cycles and the nutritional value of the resources for consumers (Peñuelas et al., 2013; Sardans et al., 2012). Nutrient supplies directly influence the stoichiometry of autotrophs, either by changing the autotroph C:X, or by changing autotroph community composition. These shifts affect primary consumers, either by changing the C:X of weakly homeostatic herbivores, or by changing herbivore community composition. Such shifts have already been observed by a number of studies (Laspoumaderes et al., 2013; Sardans et al., 2012; Teurlinckx et al., 2017). Furthermore, nutrient recycling is related to organism nutrient requirements. Animals with high P-requirements recycle low amounts of P (C:P of excretion is high), and vice versa. Here we identified that the sensitivity of consumers to nutrient imbalance varies with temperature, and that for organisms living at temperatures above their $MaxTER_{C:P}$, warming would increase their sensitivity to nutrient limitation (or C excess). These thermal changes in organism nutrient requirements should lead to changes in nutrient recycling in food webs exacerbating the impact of warming, creating simultaneous shifts in resource quality driven by alterations of biogeochemical cycles, that may create or strengthen nutritional mismatches between resources and consumers in food webs.

Although the temperature range we used in our experiments is much wider than expected by global warming (IPCC, 2014), in some extreme climatic conditions (i.e., heat waves), some freshwater ecosystems may suffer from these high temperatures. Hence, even the response to high or very low temperatures may be important to understand how extreme climatic events may affect consumer requirements. Indeed, we show that, depending on where the thermal environment sits relative to the $MaxTER_{C:P}$ temperature and the direction of change in nutrient availability, even relatively small predicted temperature increases can have strong effects on consumer performance. However, the effects of these temperature changes might be counteracted if changes in nutrient availability move in the same direction as the thermal response of nutrient requirements, i.e., further eutrophication of waters would increase P-availability. At the same time, warming would increase organism P-requirements. Based on our results, we predict that the ongoing nutrient reductions in many water bodies globally may ironically

exacerbate the impacts of warming temperatures. We propose that an accurate mechanistic understanding of the complex relationship between temperature and stoichiometric requirements of consumers is essential if we are to predict how ectotherms will respond to ongoing changes in nutrient supplies and environmental temperature.

AUTHORSHIP

C.L. conceived the idea. C.L., J.J.E., E.B., B.M., M.B. and C.L.M. conceived the study design. C.L., A.M., J.B., N.T. and G.T. performed the experiments. G.T. provided field samples. C.L., A.M. and J.B. performed all analyses. C.L., M.B. and C.L.M. wrote the manuscript with input from all other authors. All authors read and agreed on the last version of the manuscript.

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COMPLIANCE WITH ETHICAL STANDARDS

The research presented in this paper complies with the national (German) laws, and the guidelines from the directives 2010/63/EU of the European Parliament and of the Council of 22nd September 2010 on the protection of animals used for scientific purposes.

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