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RESEARCH ARTICLE

Energetic mismatch induced by warming decreases leaf litter decomposition by aquatic detritivores

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Abstract

1. The balance of energetic losses and gains is of paramount importance for understanding and predicting the persistence of populations and ecosystem processes in a rapidly changing world. Previous studies suggested that metabolic rate often increases faster with warming than resource ingestion rate, leading to an energetic mismatch at high temperature. However, little is known about the ecological consequences of this energetic mismatch for population demography and ecosystem functions.
2. Here, we combined laboratory experiments and modelling to investigate the energetic balance of a stream detritivore *Gammarus fossarum* along a temperature gradient and the consequences for detritivore populations and organic matter decomposition.
3. We experimentally measured the energetic losses (metabolic rate) and supplies (ingestion rate) of *Gammarus* and we modelled the impact of rising temperatures and changes in *Gammarus* body size induced by warming on population dynamics and benthic organic matter dynamics in freshwater systems.
4. Our experimental results indicated an energetic mismatch in a *Gammarus* population where losses via metabolic rate increase faster than supplies via food ingestion with warming, which translated in a decrease in energetic efficiency with temperature rising from 5 to 20°C. Moreover, our consumer–resource model predicts a decrease in the biomass of *Gammarus* population with warming, associated with lower maximum abundances and steeper abundance decreases after biomass annual peaks. These changes resulted in a decrease in leaf litter decomposition rate and thus longer persistence of leaf litter standing stock over years in the simulations. In addition, *Gammarus* body size reductions led to shorter persistence for both leaf litter and *Gammarus* biomasses at low temperature and the opposite trend at high temperature, revealing that body size reduction was weakening the effect of temperature on resource and consumer persistence.

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5. Our model contributes to identifying the mechanisms that explain how thermal effects at the level of individuals may cascade through trophic interactions and influence important ecosystem processes. Considering the balance of physiological processes is crucial to improve our ability to predict the impact of climate change on carbon stocks and ecosystem functions.

KEYWORDS
detritivores, ectotherms, energetic mismatch, global warming, litter decomposition, metabolic theory of ecology, temperature-size rule

1 | INTRODUCTION

Average overall surface temperature is predicted to increase by 0.2°C per decade and up to 2–5°C by the end of the century, leading to considerable perturbations at all levels of biological organization (Dawson et al., 2011; Walther et al., 2002). Temperature strongly influences life-history traits, population dynamics, species interactions and ecological processes in most ecosystems (Dell et al., 2011; Sommer et al., 2012; Woodward et al., 2010). In particular, temperature has important effects on physiological traits related to energy acquisition and expenditure (Brown et al., 2004), such as metabolic rate (Dillon et al., 2010; Marshall & McQuaid, 2011) and ingestion rate (Rall et al., 2012; Vucic-Pestic et al., 2011) which together determine the energy balance of organisms. Both metabolic and ingestion rates are expected to increase with warming with important consequences for organism fitness, trophic interactions (Bideault et al., 2020; Rall et al., 2010; Sohlström et al., 2021) and fluxes of energy and matter within and across ecosystems (Demars et al., 2011; Follstad Shah et al., 2017). Furthermore, most organisms are ectotherms (Bickford et al., 2011) that are particularly sensitive to temperature (Angilletta et al., 2002). Thus, thermal physiology of ectotherms is key to understand the response of ecosystems to global warming (Deutsch et al., 2008).

The metabolic theory of ecology (hereafter, MTE, Brown et al., 2004) provides a powerful theoretical framework to investigate ecosystem functioning in the context of global warming. The MTE combines the effects of body mass and temperature on biochemical processes to predict individual physiological performances (Gillooly et al., 2001; West et al., 2003) and scaling up from the individual to the population, community and ecosystem levels (Allen et al., 2005). As metabolic losses increase exponentially with warming, organisms generally increase energy supply through nutrient ingestion to counteract an increasing energy demand (Sentis et al., 2012; Lemoine et al., 2013). However, metabolism increases more rapidly than nutrient ingestion with temperature, which is emphasized by a higher activation energy for metabolic rate than for ingestion rate (Lemoine & Burkepile, 2012; Rall et al., 2010; Schaum et al., 2018; Sentis et al., 2012). This mismatch entails decreasing energetic efficiency (i.e. the ratio of energy acquired over energy consumed) as temperature rises (Bideault et al., 2020). Only few empirical studies directly measured the decrease in energetic efficiency with warming (Lemoine & Burkepile, 2012; Rall et al., 2010; Sohlström et al., 2021). A better assessment of the thermal dependency of energetic efficiency is urgently needed as the latter is connected to fitness in diverse ectothermic taxonomic groups (Archer et al., 2019; Donelson et al., 2010; Sentis et al., 2015, 2017).

Enhanced mismatch between physiological rates leading to reduced energetic efficiency in consumers with warming is predicted to have complex impacts on population dynamics and ecosystem processes (Bideault et al., 2020; Rall et al., 2010; Sohlström et al., 2021). For instance, empirical evidences indicate that organisms reach a smaller body size at higher temperature (i.e. temperature-size rule; Atkinson, 1994) and larger individuals are disproportionately affected by warming due to higher per capita energetic demands compared to smaller individuals (Baudron et al., 2014; Messmer et al., 2016), resulting in a decline in body sizes in ectotherm populations (Atkinson et al., 2003; Daufresne et al., 2009; Forster et al., 2012; Gardner et al., 2011). Such body size reductions would reverberate on demographic processes and their outcomes, notably food web dynamics (Osmond et al., 2017; Sentis et al., 2017) and fluxes of energy and matter (Dillon et al., 2010; Norkko et al., 2013), impacting ecosystem functioning (Dossena et al., 2012; Emmerson et al., 2005; Woodward & Warren, 2007) and resilience to perturbations (Emmerson & Raffaelli, 2004; Rip & McCann, 2011). While numerous studies on ectothermic responses to warming have focused on direct effects of body mass and temperature on biological rates, few studies focused on indirect interactive effects of changing body size with temperature on populations (Bernhardt et al., 2018; Osmond et al., 2017; Sentis et al., 2017).

Current knowledge on global warming impact on consumer–resource dynamics has primarily focused on carnivore and herbivore populations whereas much less is known on detritivore populations, despite their functional importance and putative susceptibility to warming (Boyero et al., 2012; Wenisch et al., 2017). Detritivores consume plant litter to meet their energy requirements and their metabolic and feeding activities generate wastes that support heterotrophic microbial production and primary production (Bernabé et al., 2018; Eggert et al., 2020). Leaf litter decomposition is responsible for the main fraction of the organic carbon assimilated by organisms or exported by streams and rivers (Boyero et al., 2011; Gessner et al., 1999; Graça et al., 2001) through downstream transport of particles and gaseous emissions towards the atmosphere (Battin et al., 2008, 2009). As most biological rates, leaf litter decomposition is expected to increase exponentially up to 20%

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considering both microbial and invertebrate taxa within a projected 4°C increase in mean water temperature (Follstad Shah et al., 2017). Detritivores have been suggested to have contrasting influences on the thermal sensitivity of aquatic leaf litter decomposition by either dampening (Boyero et al., 2011), enhancing (Alp et al., 2016) or having no significant effect on this process (Follstad Shah et al., 2017). However, these previous studies fall short of elucidating how thermal constraints on detritivores scale up from individuals to whole ecosystems. In this context, energy-based models provide a powerful framework to explore the consequences of global warming for consumer–resource dynamics by incorporating empirical physiological traits of individuals associated with changes in body mass and temperature into modelling simulations of population and community dynamics. Significant advances on thermal bioenergetic models have been done over the past decades (Gilbert et al., 2014; Rall et al., 2010; Synodinos et al., 2021; Vasseur & McCann, 2005) and recent studies extended the previous assumptions by including a temperature-driven change in body mass (Bernhardt et al., 2018; Osmond et al., 2017; Sentis et al., 2017), making these models a relevant approach for studying the impacts of temperature and body size changes on detritivore–resource dynamics. One key finding emerging from these modelling studies is that investigating the balance between key physiological processes that determines the fitness of detritivores (Jabiol et al., 2020) is crucial to better predict the responses of populations and freshwater ecosystems to global warming (Bideault et al., 2020; Demars et al., 2011; Yvon-Durocher et al., 2010).

In this study, we combined laboratory experiments and energy-based models to investigate thermal energetic mismatch between energy demand (i.e. metabolic rate) and supply (i.e. ingestion rate) and simulate the consequences of this thermal mismatch for seasonal population dynamics and carbon fluxes. Our laboratory experiment was designed to assess thermal reaction norms of energy demand and supply for the detritivore *Gammarus fossarum* (Koch 1836), a dominant invertebrate species in temperate headwater streams. We used individual-based experiments to examine if the mismatch in the physiological responses of individuals to warming was impacting the energetic efficiency of this keystone detritivore species. Experimental results were then used to parameterize a simplified consumer–resource model describing the seasonal dynamics of *Gammarus* and leaf litter biomasses in a temperate stream. Our model allowed us to explore the effects of temperature-induced changes in body size by simulating two scenarios of body mass reduction with temperature based on empirical observations for numerous aquatic taxa (Forster et al., 2012). If the energy demand–supply mismatch reported for herbivores and predators (Bideault et al., 2020) also holds true for detritivores, we expected metabolic rate to increase faster than ingestion rate with rising temperature, resulting in a reduction in energetic efficiency. Moreover, we predicted changes in the population dynamics of detritivores and the rate of leaf litter decomposition, where populations composed of smaller individuals were more resilient to warming but having less consumption impact on the leaf litter standing stocks.

2 | MATERIALS AND METHODS

2.1 | Biological model

The biological model used, the amphipod *G. fossarum* (Koch 1835), is a widespread crustacean species in European streams (Weiss & Leese, 2015). A large number of individuals (~500) were collected from submerged leaf litter in a pristine first-order woodland stream in the Montagne Noire, South-Western France, as in Réveillon et al. (2019). Individuals were maintained with constant oxygen supply in a cool (10°C) dark place in the laboratory for 2 weeks prior to the experiments. The water temperature for maintenance (10°C) was chosen to be close to the temperature of the sampling stream (5°C) to prevent thermal stress. No ethical permit was required under French legal requirements to conduct these laboratory experiments.

2.2 | Empirical estimation of energetic efficiency along a temperature gradient

Our laboratory experiments consisted of measuring the energetic balance between routine metabolic rate (RMR) and leaf ingestion rate (IR) for 90 individuals selected to cover a realistic spectrum of dry body mass (2.41–6.73 mg, see below for more details). At each of the six experimental temperatures (5, 8, 11, 14, 17 and 20°C), 15 individuals were tested separately for metabolic rate and ingestion rate, yielding 15 replicates per temperature. The boundaries of this thermal range corresponded to the minimal and maximal temperatures experienced by the focal population in winter and summer, respectively, in line with previous studies on this species (Becker et al., 2016; Jabiol et al., 2020; Réveillon et al., 2019). No mortality was recorded among *Gammarus* individuals during the experiments as the organisms were maintained in temperate water (i.e. no thermal stress) without food limitation (i.e. no starvation stress) and manipulated carefully. Gammarus mortality rate was null over the duration of the conditioning and the experiments (72 hr).

2.3 | Metabolic rate measurement

Routine metabolic rate was measured using a fluorescence-based multichannel respirometer (SDR SensorDish®, Presens GmbH, Germany) as in Réveillon et al. (2019). *Gammarus* were kept at ~10.0°C in the dark in individual containers, and starved for 24 hr prior transfer to the respiration chambers. Before the start of the RMR measurement, individuals of each treatment group were randomly placed in multi-dish wells filled with 3 ml of oxygen-saturated water and maintained in the dark for ~30 min for the water to reach one of the six temperature treatments before sealing the wells with a hermetic lid. Five wells on the multi-dish were used as controls for RMR by leaving them without animals. Respiration rate was measured after ~2 additional min in the dark without any manipulation of animals to avoid excessive oxygen consumption due to manipulation

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stress. Dissolved oxygen concentrations were recorded every 15 s over 40–55 min and time series were truncated at both ends in order to keep the linear portion of the oxygen depletion curves. RMR was calculated as the slope of oxygen depletion over a *ca* 35 min timeframe, corrected for the mean linear trend over time of oxygen concentration in controls as follows: $RMR = (c_i - c_f)/(t_i - t_f)$, where c_i and c_f are initial and final oxygen concentrations (µmol O_2/L) in the wells and t_i and t_f are initial and final times points (day^{-1}) of the respiration experiment. Values were converted into C release rate (µg C/day) assuming a respiratory coefficient of 0.78 (as estimated for *Gammarus pulex*, Wright & Wright, 1979).

2.4 | Leaf litter ingestion rate measurement

Leaf litter substrate was composed of ash leaves *Fraxinus excelsior*, an abundant species contributing to allochthonous inputs in temperate forest streams and consumed by *Gammarus* (Lewis et al., 2017; Nelson, 2011). Freshly fallen ash leaves were collected 1 month prior to the experiments in a similar first-order stream of the same geographical area where *Gammarus* individuals were collected. Leaves were then dried and stored at −15°C in the laboratory. Prior to the experiment, dried leaves were conditioned for 2 weeks in a tank filled with 10 L of continuously oxygenated water from the sampled stream. This allowed leaves to be colonized and partly decomposed by fungi (aquatic hyphomycetes) to simulate the conditions encountered by *Gammarus* in streams (Jabiol & Chauvet, 2012). Then, leaves were washed with pristine water and cut into 1-cm diameter discs, avoiding the central vein that is less edible for *Gammarus*. Following the RMR measurement, *Gammarus* were put in individual arenas (10 × 7 × 3.5 cm) filled with 100 ml of oxygen-saturated water maintained at the same temperature as in the respirometer chamber. The individual arenas were partly immersed in either of the six temperature-controlled water baths maintained at the desired temperature. *Gammarus* were allowed to explore the experimental arena for ~2 min before the experiment to reduce manipulation stress. Ingestion rate (IR) was measured by allowing individuals to feed on pre-weighed batches of six dry leaf discs (mean ± *SD*: 10.25 ± 0.68 mg) for 48 hr in dark conditions. Leaf discs were visible in the individual arenas and consumption time was sufficient as a significant fraction of leaf discs was consumed in the low temperature treatments. Background leaf mass loss not attributed to litter ingestion by *Gammarus* was estimated in five control arenas without animals for each of the six temperature treatments. At the end of the feeding experiment, individuals and leaf discs were frozen at −15 °C, freeze-dried for 24 hr and weighed to the nearest 0.001 g. Litter ingestion rate (µg C/day) was calculated as follows: $IR = (m_i \times c - m_f) \times \chi / t$, where m_i and m_f are initial and final mass (µg) of dried leaf discs from arenas with animal, respectively, c is the mean ratio of final to initial mass of leaf discs allowed to decompose for 48 hr in the absence of *Gammarus* at each temperature, χ is the conversion factor (0.45) of dry mass to C content of leaf litter (Lecerf & Chauvet, 2008) and t is the duration (day) of the feeding experiment.

2.5 | Statistical analysis

The following equations were used to express the mass (M in mg) and temperature (T in Kelvin) dependence of individual *RMR* and *IR* (Brown et al., 2004; Englund et al., 2011):

$$I = \alpha M^b e^{Ea\left(\frac{T-T_0}{k_B T_0 T}\right)}, \quad (1a)$$

$$I = \alpha M^b e^{p\left(\frac{T-T_0}{k_B T_0 T}\right) - q\left(\frac{T-T_0}{k_B T_0 T}\right)^2}, \quad (1b)$$

where α is the metabolic or the ingestion expression level at the reference temperature (T_0), b is the mass-scaling exponent, M is the dry body mass (mg), Ea is the activation energy (eV) and k_B is the Boltzmann's constant (8.62×10^{-5} eV K^{-1}). The quadratic equation within the exponential term (Equation 1b) is a deviation of the MTE expression allowing to investigate the curvature strength of the relationship between the measured rate (I) and temperature, where p and q were fitted polynomial first- and second-order terms describing the curvature respectively (Englund et al., 2011; Irlich et al., 2009). T_0 was set to 12.5°C (i.e. the mean of the values of experimental temperatures) while parameters α, b, p and q were estimated for metabolic and ingestion rates using polynomial regressions of log-transformed metabolic or ingestion rates on log-transformed body masses and standardized inverse temperatures (i.e. $1/k_BT - 1/k_BT_0$). To assess the best fitting estimations, we computed two generalized linear models on Eq 1 for both metabolic and ingestion rates: a first model including the quadratic formulation of the MTE (Equation 1b) and a second model including a standard MTE formulation (Equation 1a). The latter is simply a particular case of the quadratic formulation where $q = 0$ and the equation is reduced to the MTE model where p can thus be interpreted as the activation energy (Englund et al., 2011). Both models were compared with a likelihood ratio test and p values were used to determine the best fitting model and the significance of parameters.

Energetic efficiency was also calculated as follows: $E = (IR/RMR) \times A_T$, where the ratio of IR to RMR is the ingestion to metabolism efficiency and A_T is the assimilation efficiency at temperature T. We expressed the temperature (T in Kelvin) dependence of assimilation efficiency using empirical equations and values for detritivores from Lang et al. (2017). Assimilation efficiency was following a logistic equation with the MTE equation both at the numerator and the denominator. With this formulation, assimilation efficiency is confined between 0 and 1 (no or complete assimilation) (Equation 2):

$$A_T = \frac{\alpha e^{Ea\left(\frac{T-T_0}{k_B T_0 T}\right)}}{1 + \alpha e^{Ea\left(\frac{T-T_0}{k_B T_0 T}\right)}}, \quad (2)$$

where α is the normalization constant of assimilation efficiency, Ea is the activation energy (eV) and k_B is the Boltzmann's constant (8.62×10^{-5} eV K^{-1}). Lang et al. (2017) provided an estimate of E_a (0.1640 eV) derived from a dataset of assimilation efficiencies for detritivores and we rescaled the intercept α (−0.8473) to obtain an assimilation efficiency value of 0.30 at the reference temperature (12.5°C).

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This translated into A_T values ranging from 0.26 at 5°C to 0.36 at 25°C. Because there is not yet a consensus on the temperature dependence of assimilation efficiency, we also investigated scenarios where assimilation efficiency was temperature independent with a constant value of 0.40 (Gergs & Rothhaupt, 2008, Figures S3 and S4). The relationship between temperature and energetic efficiency was estimated using a linear regression. Four outliers (one at 5°C, one at 8°C and two at 20°C) were excluded from the analyses due to unrealistic very distant metabolic and ingestion rate values from the fitted curves (residual values >3 μg C/day). Statistical analyses were computed using the R software v.3.3.4 (R Development Core Team, 2018). Generalized linear regressions were computed using the *glm* function and were compared using the *anova* function from the STATS R package and *lrt* function from the LMTEST R package.

2.6 | Modelling consumer–resource dynamics

We developed a mathematical consumer–resource model parametrized using our experimental estimates of ingestion and metabolism rates to describe the dynamics of *Gammarus* and leaf litter biomasses in streams. All individuals were assumed to have the same body mass (i.e. population size structure was not implemented) as we intended to focus on carbon biomass dynamics and did not have enough information about the temperature and body mass dependences of *Gammarus* life-history traits to implement a size-structured population model. Changes in *Gammarus* population biomass were driven by the balance between carbon intake through food ingestion and carbon loss through respiration in animals while changes in leaf litter biomass were due to *Gammarus* herbivory pressure on a seasonal litterfall stock (Yodzis & Innes, 1992). Below is the system of ordinary differential equations describing temporal change in leaf litter standing stocks (L) and *Gammarus* population biomass (G) (Equation 3a and 3b).

$$\frac{dL}{dt} = I - f(L)_T G - k_T L, \tag{3a}$$

$$\frac{dG}{dt} = G\left[f(L)_T A - RMR_T\right]. \tag{3b}$$

Leaf litter standing stock is sustained by litter inputs (I) and decreases due to *Gammarus* population feeding activity ($f(L)_T$ A_T G) and other degradation processes (e.g. microbial decomposition and leaching) of litter decomposition (k_T L). $f(L)_T$ is the temperature-dependent functional response of *Gammarus* population (mg C mg C^{-1} day^{-1}) and k_T is a temperature-dependent rate of litter mass loss (day^{-1}) owing to microbial decomposition and leaching (e.g. Alp et al., 2016). A_T is the temperature-dependent assimilation efficiency of *Gammarus* calculated using the activation energy and mass-scaling exponent proposed in Lang et al. (2017) for detritivores in Equation 2 (see Supplementary Material for a constant assimilation efficiency). Leaf litter inputs were specified as discrete events occurring once at the beginning of each year (see below for more details) simulating leaf fall in autumn. Biomass dynamics of the *Gammarus* population was described as a balance of C intake through litter ingestion and loss through respiration with RMR_T is the RMR (mg C/day) estimated using the activation energy and mass-scaling exponent for metabolic rate of the experimental population in Equation 1a.

Gammarus feeds on leaf litter following a Holling type II functional response (Equation 4).

$$f(L)_T = \frac{a_T L}{1 + a_T h_T L}. \tag{4}$$

where a_T and h_T are the attack rate of *Gammarus* on leaves (m^{-2}/day) and the handling time (day^{-1}) at temperature T, respectively, and L is the leaf litter biomass (mg C/m^2). Attack rate and handling time were derived using the quadratic term and mass-scaling exponent for ingestion rate of the experimental population in Equation 1a. Derivations of these parameters are further detailed in the Supplementary Materials.

Leaf litter is also affected by microbial decomposition which is responsible for a large part of the carbon fluxes in aquatic ecosystems (Schneider, 2012). We used the Arrhenius equation to express the temperature dependence of microbial decomposition rate (Equation 5).

$$k_T = k_{10°C} e^{-E_a\left(\frac{1}{k_B T} - \frac{1}{283.15 k_B}\right)}, \tag{5}$$

where $k_{10°C}$ is litter decomposition rate at 10°C (i.e. 283.15 K), E_a is the activation energy (eV) and k_B is the Boltzmann's constant. Follstad Shah et al. (2017) provided in situ estimates of E_a (0.3700 eV) and $k_{10°C}$ (0.0096 day^{-1}) deriving from data of litter decomposition in fine mesh bags.

In our model, initial conditions for litter standing stock (L) and *Gammarus* biomass (G), as well as the amount of annual litterfall, were selected based on previous observations of streams from the region where animals originated (Lecerf et al., 2005). Initial value for litter standing stock was set to 300,000 mg C/m^2 and annual leaf litter input to 300,000 mg C m^{-2} $year^{-1}$. Litterfall occurred evenly over 15 consecutive days, so as to mimic the phenology of forest vegetation in the study region. Initial value for *Gammarus* biomass (G) was set to 30 mg dry mass m^{-2} (i.e. 15 mg C/m^2) and *Gammarus* mean individual body mass was 4.26 mg dry mass based on the animals we used in the laboratory experiment. These values were considered as the reference scenario (i.e. TSR_R) where the *Gammarus* mean body mass is constant across temperatures. Because body mass of organisms is temperature dependent (TSR, Atkinson, 1994), we also investigated the effects of temperature-induced changes in the mean body mass of the detritivore population on the carbon stocks dynamics by simulating three body size reduction scenarios following Forster et al. (2012) and detailed in the Supplementary Materials (TSR_R, TSR_A and TSR_M).

The dynamics of litter standing stocks and *Gammarus* population biomass were simulated at five different water temperatures (5, 10, 15, 20 and 25°C) for each of the three TSR scenarios (TSR_R, TSR_A and TSR_M) for a duration of 7 years. The first year of each simulation

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was excluded because of transient dynamics following the input of leaf litter and detritivores in the system. Starting values of the other parameters mentioned above (i.e. leaf litter and *Gammarus* biomass) were constant among TSR scenarios as we primarily focused on the relationship between body mass and temperature (but see Supplementary materials Figure S2 for the influence of changing the starting values of these parameters). We defined a lower threshold for litter standing stock following Alp et al. (2016) (i.e. 20% of initial biomass, 6×10^4 mg C/m^2) and a lower threshold for *Gammarus* stock (i.e. 5×10^3 mg C/m^2). We calculated the mean annual persistence time above these thresholds over the 6 years period from the model outputs. We also fragmented time series in consumer–resource cycles (i.e. time between two consecutive biomass peaks) and calculated the slope of biomass decrease over time from peaks to thresholds of the cycles using a linear regression.

Simulations were obtained by solving the ordinary differential equations system using the *ode* function from the deSolve R package (Soetaert et al., 2010). Graphics were obtained using the ggplot2 R package (Wickham, 2016).

3 | RESULTS

3.1 | Empirical estimation of energetic mismatch

We experimentally investigated the relationships between metabolic and ingestion rates with body mass and temperature over a 5–30°C gradient. We found that the polynomial model with quadratic term for thermal dependency (Equation 1b) described more accurately the temperature dependence of RMR (Anova, $F_{1,81} = 15.41$, $p<0.001$) and ingestion rate (Anova, $F_{1,81} = 5.61$, $p = 0.0202$) in *G. fossarum* than the standard MTE model (without quadratic term). This was also indicated by significant Likelihood ratio tests between the two functions for metabolic rate (Chi-square test, $\chi^2 = 5.70$, $p = 0.0170$) and ingestion rate (Chi-square test, $\chi^2 = 5.81$, $p<0.01$). Both RMR and ingestion rate increased with warming [$CI_{2.5\%} - CI_{97.5\%}$], ranging from 10.00 [8.39–11.62] to 50.79 [44.30–57.28] µg C/day and from 388.83 [291.98–485.69] to 793.13 [681.39–904.86] µg C/day respectively (Figure 1). We estimated a lower mass-scaling exponent value for RMR than for ingestion rate (0.62 [0.41–0.84] and 0.82 [0.50–1.13] respectively) while the curve steepness was higher for RMR than for ingestion rate (0.67 [0.60–0.74] and 0.32 [0.22–0.42] respectively). Estimates of quadratic terms were similar between these rates (0.21 [0.11–0.32] and 0.19 [0.03–0.35] respectively, Table 1). Overall, we showed that metabolic rate increases faster than ingestion rate with warming (Figure 1), indicating a thermal energetic mismatch between energy expenditure and intake. This energetic mismatch was confirmed by the negative relationship between energetic efficiency and temperature ($F_{1,83} = 23.58$, $p<0.001$), which decreased by twofold from 5 to 20°C (10.94 [7.60–14.28] to 5.46 [4.46–6.47], Figure 2). Our results were qualitatively similar when assimilation efficiency was considered as temperature independent (Figures S3 and S4) although the energetic mismatch was stronger for results with temperature-dependent assimilation efficiency.

3.2 | Modelling consumer–resource dynamics

The predictions from the consumer–resource model highlighted two major results: a warming effect and a body mass reduction effect on consumer–resource dynamics. First, we found a common pattern across TSR scenarios on the seasonal dynamics of carbon stocks. Focusing on the reference scenario without body size changes (TSR_R), leaf litter stock was decreasing until almost complete disappearance before the next annual litterfall while *Gammarus* stock was following

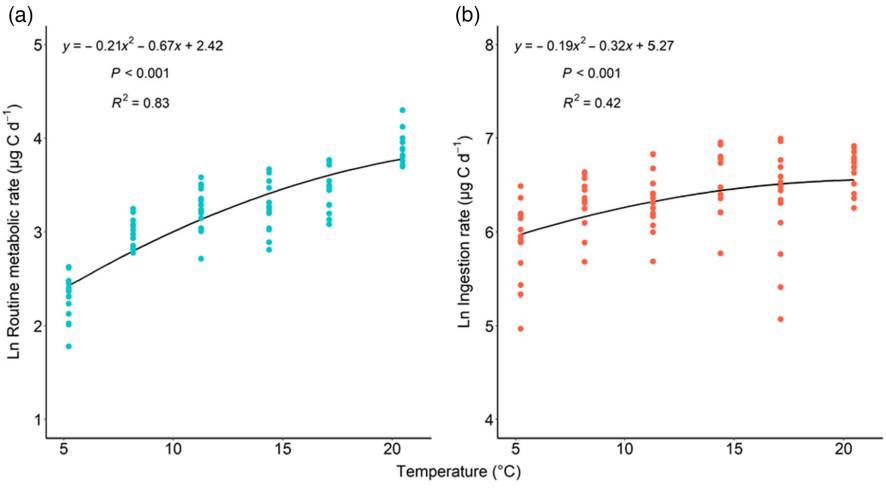


FIGURE 1 Nonlinear thermal reaction norms of (a) routine metabolic rate (log-transformed) and (b) ingestion rate (log-transformed) as a function of temperature for *Gammarus* individuals ($n = 86$). Regression lines estimated from linear models on the polynomial formulation of the MTE were represented (black line) with equations, significance (p) and regression coefficient (R^2). Equation coefficients were estimated using the Arrhenius formulation of the MTE with the inverse temperature normalized to the reference temperature (12.5°C)

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TABLE 1 Parameter estimates and significance extracted from quadratic linear models for routine metabolic rate (RMR) and ingestion rate (IR) at 12.5°C: Intercept (*I*), body mass-scaling exponent (*b*), steepness of the relationship (*p*) and quadratic term (*q*). Significance was estimated with an ANOVA test (*t* and *p* values; see Section 2). Negative quadratic terms originated from the fitting of the quadratic model with a Boltzmann formulation so that high negative *p* and *q* values indicated a high curvature of the relationship

	Parameter	Estimate	*t*	*p*
Routine metabolic rate (RMR)	Intercept	2.42	15.78	<0.001
	Mass exponent (*b*)	0.62	5.73	<0.001
	Curve steepness (*p*)	−0.67	−19.48	<0.001
	Quadratic term (*q*)	−0.21	−3.93	<0.001
Ingestion rate (IR)	Intercept	5.27	23.22	<0.001
	Mass exponent (*b*)	0.82	5.07	<0.001
	Curve steepness (*p*)	−0.32	−6.28	<0.001
	Quadratic term (*q*)	−0.19	−2.37	0.0202

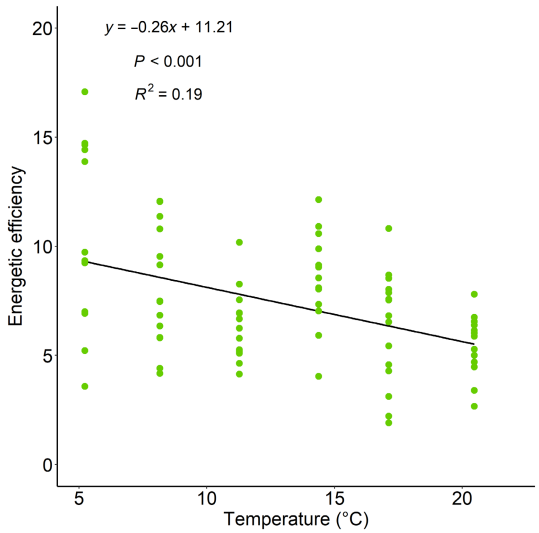


FIGURE 2 Linear thermal reaction norms of energetic efficiency as a function of temperature for *Gammarus* individuals ($n = 86$). Energetic efficiencies were calculated using log-transformed routine metabolic rate and ingestion rate. The regression line estimated from a linear model was represented (black line) with equation, significance (*p*) and regression coefficient (R^2)

the same dynamics with a phase lag due to the time needed to consume leaf litter and reproduce (Figure 3 and Figure S1). However, our simulations showed a decrease in *Gammarus* biomass and persistence with warming, which was characterized by lower maximum values (Figure S1) and steeper decreases after population peaks (e.g. -0.26×10^3 and -1.17×10^3 mg C m^{-2} day^{-1} for TSR_R respectively at 5°C and 25°C, Figure 3b). This resulted in an increase in leaf litter biomass and persistence, which was characterized by higher maximum values (Figure S1) and smoother decreases after litterfall peaks (e.g. $-1.0.06\times10^4$ and -0.46×10^4 mg C m^{-2} day^{-1} for TSR_R respectively at 5°C and 25°C, Figure 3a). Overall, warming negatively impacted the *Gammarus* population (Figure 4b) and consequently led to the accumulation of the leaf litter stock over time (Figure 4a).

Second, we showed that a changing mean body mass with temperature (TSR scenarios) led to noteworthy differences in the dynamics of the carbon stocks depending on TSR strength. Concerning the detritivore consumer, the annual persistence time for *Gammarus* significantly decreased at temperature between 5 and 15°C but tended to be longer at higher temperatures (mostly at 25°C) for all TSR scenarios (Figure 4b). However, when comparing the different temperature-size responses, we found that persistence time for the average TSR_A and the maximum TSR_M scenarios was lower than for the reference scenario (TSR_R) at low temperatures (e.g. 197 and 290 days at 5°C respectively for TSR_M and TSR_R) but became higher than the reference scenario TSR_R for temperatures above 15°C (e.g. 153 and 77 days at 25 °C respectively for TSR_M and TSR_R). Moreover, the decrease in persistence time at high temperatures was particularly pronounced for the maximum TSR_M scenario to the extent that persistence times were almost similar to the ones at low temperatures (i.e. forming a U-shaped curve). Concerning the litter resource, the annual persistence time for leaf litter showed a contrasting pattern compared to the *Gammarus* population and significantly increased with temperature across the 5–30°C gradient (Figure 4a). Moreover, leaf litter persistence time for the TSR_A and the TSR_M scenarios was lower than the reference scenario TSR_R at low temperatures (e.g. 19 and 22 days at 5°C respectively for TSR_M and TSR_R) but became higher than the reference scenario TSR_R for temperatures above 15 °C (e.g. 83 and 71 days at 25°C respectively for TSR_M and TSR_R). Overall, our modelling results showed that warming and body mass reduction were impacting the dynamic of a consumer–resource system. *Gammarus* biomass was negatively affected by warming, although this negative effect was weaker at high temperature for TSR scenarios with a strong body mass reduction, which allowed the *Gammarus* population to persist for a longer time. Conversely, leaf litter biomass was positively affected by warming due to reduced ingestion by *Gammarus* populations with smaller biomasses at high temperature and a strong body mass reduction reinforced the effect of warming, leading to accumulation of leaf litter for a longer time.

To summarize, we found an energetic mismatch between metabolic and ingestion rates, where costs increased faster than supplies with warming, which translated into a decrease in energetic efficiency and had significant effects on our model simulations. Indeed, this mismatch caused a reduction in the detritivore biomass with warming because of an unbalance between energy demand and supply (i.e. reduced energetic efficiency). Consequently, leaf litter standing stock was processed by fewer detritivores leading to leaf

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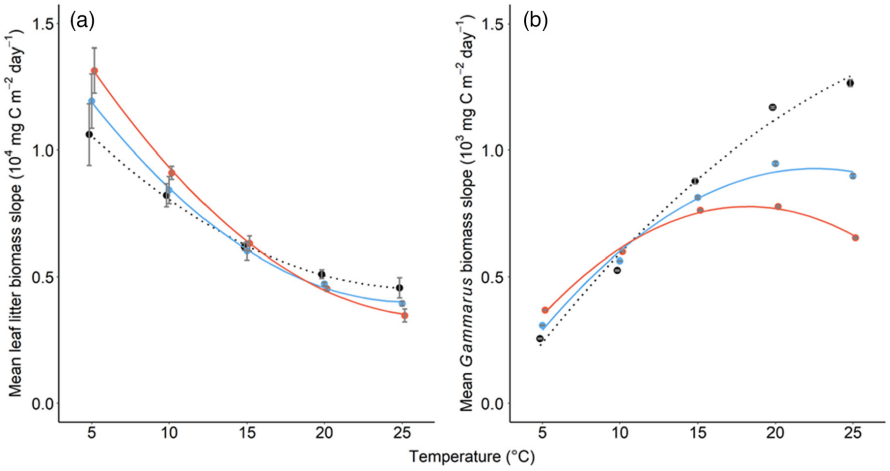


FIGURE 3 Mean slope of biomass decreases after maximum biomass peak (absolute value) of (a) leaf litter stock and (b) *Gammarus* stock. Mean slopes were estimate over six consumer–resource cycles as a function of water temperature for the three different temperature-size scenarios: The reference scenario (i.e. TSR_R, black dotted line), the average TSR scenario (i.e. TSR_A, blue solid line) and the strong TSR scenario (i.e. TSR_M, red solid line). Dots represent the slope values and lines were obtained by smoothing the curves linking the dots. Error bars (grey bars) correspond to standard deviations estimated for each temperature and temperature-size scenario over 6 years

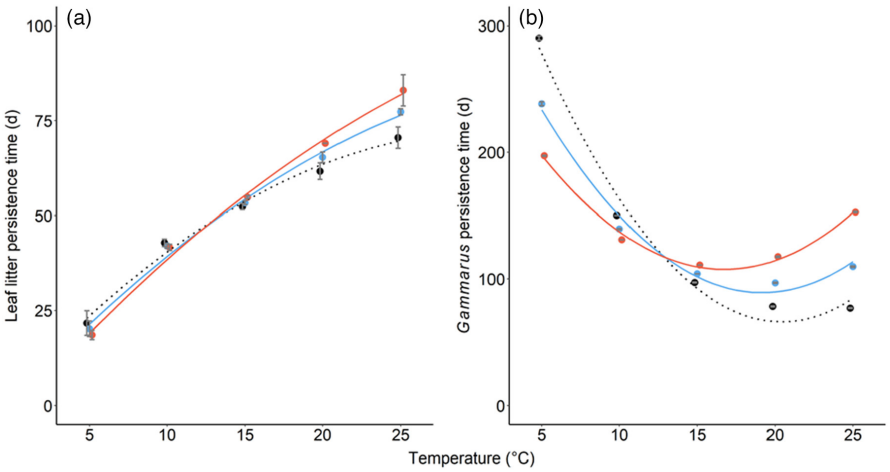


FIGURE 4 Mean annual number of days (a) above the 20% threshold (6×10^4 mg C/m^2) for leaf litter stock and (b) above the 5% threshold (5×10^3 mg C/m^2) for *Gammarus* stock. Mean numbers of days were estimated over 6 years as a function of water temperature for the three different temperature-size scenarios: The reference scenario (i.e. TSR_R, black dotted line), the average TSR scenario (i.e. TSR_A, blue solid line) and the strong TSR scenario (i.e. TSR_M, red solid line). Dots represent the biomass values and lines were obtained by smoothing the curves linking the dots. Error bars (grey bars) correspond to standard deviations estimated for each temperature and temperature-size scenario over 6 years

litter accumulation over time. In other words, warming leads to a significant reduction in the decomposition of leaf litter mediated by detritivores. Moreover, the slight increase in detritivore biomass at high temperature due to lower energetic demands in the case of body mass reduction did not compensate for the reduced leaf litter ingestion of a detritivore population having a lower mean body mass. This pattern was more or less amplified when considering different temperature-size responses for detritivore populations: a strong decrease in mean body mass (TSR_M) inhibited even more leaf litter decomposition than a moderate decrease in body size (TSR_A) with warming.

4 | DISCUSSION

Estimating the thermal sensitivity of physiological rates that determine the energetic balance of ectotherm organisms is crucial to predict the responses of populations and ecosystem processes to global warming (Sinclair et al., 2016). Under the MTE, warming should not affect the energy balance of organisms as energetic gains and costs should increase with warming at the same pace. In contrast to the MTE predictions, our simultaneous measurements of metabolic rate and ingestion rate on the detritivore species *G. fossarum* indicated that this assumption does not hold

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true. We found that the relationship with temperature was more than twofold steeper for RMR (0.67 eV) compared to ingestion rate (0.32 eV), hinting at a higher thermal sensitivity of metabolism than food ingestion. Warming is likely to increase energetic costs of ectothermic organisms through an exponential increase in metabolic rate (Gillooly et al., 2001). In turn, increased metabolic demands may affect other biological rates, representing energetic expenditures, such as growth and reproduction (Watts et al., 2011; Ohlberger, 2013), or energetic supplies, such as food ingestion (Rall et al., 2010, 2012). In particular, ectotherm organisms are expected to increase ingestion rate of resources to meet their higher energy requirements at higher temperatures (Hillebrand et al., 2009; Vucic-Pestic et al., 2011). Our results and previous studies demonstrated that resource consumption does not follow the pace of increasing metabolism with warming, constituting an energetic mismatch where energetic costs become increasingly important compared to energetic supplies (Lemoine & Burkepile, 2012; Lindmark et al., 2018; Rall et al., 2010). For example, Rall et al. (2010) also reported activation energies more than twofold higher for metabolic rate than for ingestion rate in beetles and spiders (0.80–0.87 eV and 0.24–0.30 eV respectively). In line with observations made on activation energies, some studies showed a decrease in ingestion efficiency with warming as a consequence of the energetic mismatch (Lemoine & Burkepile, 2012; Rall et al., 2010; Vasseur & McCann, 2005). Our results also particularly underpinned the temperature-driven energetic mismatch by showing the decrease in the energetic efficiency (i.e. the proportion of C incorporated per unit of C respired) by threefold with a 15°C increase in temperature. Declining energetic efficiency with warming has been linked to fitness reduction across a large variety of taxonomic groups (Amarasekare & Savage, 2012; Donelson et al., 2010; Lindmark et al., 2018). Such fitness reductions may have profound impacts on the dynamics of ectotherm populations (Deutsch et al., 2008) and ecosystem processes (Allen et al., 2005).

Understanding the thermal sensitivity of detritivore-mediated leaf litter decomposition is of major importance to assess the impacts of global warming on freshwater ecosystems. Our consumer–resource model predicts that the detritivore biomass is declining with warming causing leaf litter stocks to accumulate with lower persistence times for *Gammarus* and higher persistence times for leaf litter with warming. This long-term pattern confronts the widespread observations of an overall increased litter decomposition by microbes and detritivores with warming in aquatic ecosystems (Ferreira & Canhoto, 2013, 2015; Ferreira & Chauvet, 2011; Griffiths & Tiegs, 2016). Indeed, the rate of leaf litter decomposition is increasing exponentially on the short-term with temperature in the same manner as biological processes (Boyero et al., 2011) because leaf litter constitutes the raw substrate supporting energetic requirements of microbes and detritivores (Gessner et al., 1999). Along the same line, Follstad Shah et al. (2017) documented that litter decomposition by microbes and detritivores can be approximated through the thermal sensitivity of enzymatic catabolic activities and is expected to increase significantly with warming. However, most of the previous studies estimated litter decomposition on restricted temporal (i.e. a few weeks or months) and spatial scales (i.e. litter patches) that did not allow for the incorporation of dynamics of detritivore populations (Boyero et al., 2011; Griffiths & Tiegs, 2016). Particularly, variation in detritivore biomass with temperature can play a crucial role (Hines et al., 2016) because the thermal dependencies of biological rates and population growth rate are connected for ectotherms (Savage et al., 2004). In our simulations, the significant decline in detritivore biomass with warming relied on the lower uptake and conversion of leaf litter into *Gammarus* biomass in relation to the higher routine metabolic activities. More generally, energy-limited detritivores will be expected to limit investments in biomass production (i.e. growth and reproduction) while the higher proportion of energetically deficient individuals will cause mortality to increase (Amarasekare & Savage, 2012; Angilletta et al., 2004; Savage et al., 2004). Therefore, this could potentially accentuate the observed lower biomass of detritivores resulting in less leaf litter decomposition with warming.

One major effect of global warming is the reduction of the body size of both terrestrial and aquatic ectotherms (Daufresne et al., 2009; Gardner et al., 2011). According to the temperature-size rule (TSR), body size decreases at the individual level due to a thermal sensitivity difference between development rate and growth rate, leading organisms to reach maturity earlier at smaller sizes. A consequent shift in the mean body size of populations is likely to have a feedback effect on population dynamics (Riemer et al., 2018), changing demographic processes (Barneche et al., 2016; Savage et al., 2004) and trophic interaction strengths (Ohlberger et al., 2011; Sentis et al., 2017). Our results further highlighted that temperature-induced body mass reduction can influence the impact of temperature on the detritivore population dynamics. *Gammarus* populations on average composed of smaller individuals (i.e. facing a body size reduction with warming) maintained a relatively high biomass for a longer period of time than populations composed of larger individuals at high temperatures. This observation appeared as directly linked to the scaling relationships of biological rates with body mass and temperature (Brown et al., 2004) combined with the energetic mismatch between metabolic losses and resource supplies discussed above. We found mass-scaling exponents lower than 1 for metabolic rate (0.62) and ingestion rate (0.82), which indicated that small individuals have higher energetic demands and supplies per unit of biomass compared to large individuals (Hou et al., 2008), the latter have nevertheless higher per capita energy demands and supplies (Baudron et al., 2014; Messmer et al., 2016). This energetic superiority of small individuals under severe warming conditions allows them to allocate more energy to growth and reproduction even in low energetic efficiency conditions whereas large individuals would starve to death (Persson & de Roos, 2006). Such a competitive advantage could then be translated into *Gammarus* populations with higher biomass persisting for a longer time when composed of small individuals (Wenisch et al., 2017). Nevertheless, these small-bodied populations decompose a smaller fraction of the leaf litter standing stock than large-bodied populations with rising temperatures

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because their numerical superiority cannot compensate for their physiological limitations due to reduced body mass. Although small individuals have a higher energetic efficiency than large individuals with warming, the former also ingest substantially less leaf litter on a per capita basis. Accordingly, we found a high mass-scaling exponent for ingestion rate (0.82) indicating a strong effect of body mass on ingestion and depletion of leaf litter stocks. Therefore, the evidence that an overall inhibition of leaf litter ingestion due to TSR mechanisms was not counteracted by an increase in population biomass and a longer persistence clearly indicated that the negative effect of body mass-related biological processes in individuals exceeded the positive effect of population abundance on leaf litter decomposition by detritivores with warming.

This study demonstrated an energetic mismatch between metabolic and ingestion rates for detritivore invertebrates that, combined with the widespread body size reduction experienced by ectotherms with warming, may have sizable repercussions on detritivore populations and leaf litter decomposition in freshwater ecosystems. Negative temperature effects on detritivore population size and litter decomposition rate reported here are consistent with previous findings showing that aquatic detritivores are scarce in warm streams compared to cool streams (Boyero et al., 2011; Foucreau et al., 2014) and invertebrates can mediate negative effects of warming on litter decomposition (Bernabé et al., 2018). Moreover, our findings conform to the widespread evidence that temperature stimulates aquatic decomposition, irrespective of whether detritivores are abundant or scarce (Alp et al., 2016; Follstad Shah et al., 2017; Galic & Forbes, 2017; Graça et al., 2015). However, the discrepancy between model simulations and the expected pattern derived from experiments may illuminate the critical role of thermal acclimation and adaptation processes in impeding a temperature-induced energetic mismatch and ensuring population persistence under warming conditions (Schaum et al., 2018; Sentis et al., 2015; Sohlström et al., 2021). Further studies have also emphasized the importance of food quality and diversity as compensatory feeding by herbivores affects the thermal response of feeding rate, which has consequences for the energetic balance (Follstad Shah et al., 2017; Hillebrand et al., 2009; Ott et al., 2012). Therefore, assessing the thermal sensitivity of microbial decomposers appears essential as microbial activities have a significant contribution to litter decomposition and modulate the food palatability and quality for invertebrate detritivores (Jabiol et al., 2020). Moreover, behavioural traits such as foraging movement are also temperature dependents and relate to the energetic balance (Cloyed et al., 2019). Overall, this study revealed the strong relationship between the thermal dependency of the energetic balance in ectotherms and predictions on the dynamics of detritivore populations and leaf litter decomposition in freshwaters with global warming.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

Tom Réveillon and Arnaud Sentis compiled the first ideas, and Tom Réveillon, Thibaut Rota, Arnaud Sentis, Antoine Lecerf and Eric Chauvet designed the experiments. Tom Réveillon performed fieldwork, laboratory experiments and statistical analyses with the assistance of Thibaut Rota, Antoine Lecerf, and Arnaud Sentis. Tom Réveillon wrote the first drafts of the manuscript, which benefited from contributions of all authors until its final form. All authors gave final approval for publication of this manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.jh9w0vtdj) (Réveillon et al., 2022).

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