

LETTER

Temperature-dependent body size effects determine population responses to climate warming

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Abstract

Current understanding of animal population responses to rising temperatures is based on the assumption that biological rates such as metabolism, which governs fundamental ecological processes, scale independently with body size and temperature, despite empirical evidence for interactive effects. Here, we investigate the consequences of interactive temperature- and size scaling of vital rates for the dynamics of populations experiencing warming using a stage-structured consumer-resource model. We show that interactive scaling alters population and stage-specific responses to rising temperatures, such that warming can induce shifts in population regulation and stage-structure, influence community structure and govern population responses to mortality. Analysing experimental data for 20 fish species, we found size–temperature interactions in intraspecific scaling of metabolic rate to be common. Given the evidence for size–temperature interactions and the ubiquity of size structure in animal populations, we argue that accounting for size-specific temperature effects is pivotal for understanding how warming affects animal populations and communities.

Keywords

Allometric scaling, climate change, communities, consumer-resource dynamics, dynamic modelling, food webs, intraspecific competition, metabolic rate, predator–prey interactions, size structure.

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INTRODUCTION

Body size and temperature are two fundamental factors on which nearly all biological rates and therefore ecological processes depend. This link is captured in the metabolic theory of ecology (MTE) (Gillooly *et al.* 2001; Brown *et al.* 2004), which predicts that metabolic rate, B , scales with mass and temperature according to $B = b_0 M^b e^{-E/kT}$, where $b_0(T)$ is a normalisation constant, b is an allometric exponent equaling 0.75, $T[K]$ is the temperature, $k[eV K^{-1}]$ is Boltzmann's constant and $E[eV]$ is the activation energy (West *et al.* 1997, 1999; Brown *et al.* 2004). Hence, an implicit assumption of the MTE is that temperature affects individual metabolism independently of body size. However, both empirical and theoretical work suggests that temperature affects the allometric exponents of vital rates, meaning that temperature effects are size specific (Strong & Daborn 1980; Xie & Sun 1990; Angilletta & Dunham 2003; Kozłowski *et al.* 2004; Glazier 2005; Killen *et al.* 2010; Ohlberger *et al.* 2012; Verberk & Atkinson 2013). As all animal populations are size structured to some degree and governed by size-dependent processes, size-specific temperature effects could induce changes in the dynamics, regulation and size structure of populations in warming environments.

Single species studies on intraspecific scaling of metabolism in relation to mass and temperature have revealed that allometric exponents can have a negative (Beamish 1964; Xie & Sun 1990; Ohlberger *et al.* 2012), positive (Newell 1973) or no (Ohlberger *et al.* 2012) relationship with temperature. In a meta-analysis of intraspecific mass–scaling relationships in teleost fishes, Killen *et al.* (2010) found strong support for a

negative temperature dependence of allometric exponents of metabolic rate across species. Several hypotheses have been developed to explain the predominantly negative temperature effects on metabolic exponents. Xie & Sun (1990) suggested that the exponent of metabolism lies between 2/3 and 1 based on the scaling of surfaces and volumes, respectively, and that increasing ambient temperatures strengthen the influence of surface-related processes, such as maintaining homeostatic balance. Based on similar boundary-related mechanisms, the metabolic-level boundary hypothesis suggests that the metabolic intensity (level) modulates the influence of the surface area- and volume-related resource demand in constraining metabolism (Glazier 2005, 2010, 2014). It has also been suggested that cool temperatures increase viscosity and reduces the boundary layer, which can result in larger respiratory costs of small compared to large organisms that are not as affected by viscosity (Verberk & Atkinson 2013). These findings all suggest that temperature effects on the size dependence of individual metabolism may be widespread in nature.

Alongside temperature, the role of body size in ecology is striking, as all organisms develop and increase in body size during ontogeny. Within populations, individuals differ in their efficiency to exploit a shared resource, due to differing size dependence of feeding ability and metabolism (Byström & Andersson 2005; Persson & de Roos 2013). Individuals with the most efficient net biomass production (difference between energy intake and metabolic costs) are superior competitors on a shared resource. Such size-based competitive asymmetry is referred to as ontogenetic asymmetry, which results in juvenile and adult growth becoming unequally limited by food availability. Because assimilated energy not used for

maintenance is primarily allocated to somatic growth in juveniles and to reproductive growth in adults, this leads to biomass being accumulated in the least efficient life stage (in terms of producing biomass), which then constitutes a population bottleneck. In other words, ontogenetic asymmetry implies that the population is regulated by either juvenile maturation or adult reproduction, depending on which of these two rates is smaller in terms of biomass density per unit time (Persson & de Roos 2013; de Roos & Persson 2013).

Ontogenetic asymmetry and the resulting mode of population regulation have major community-wide implications (de Roos & Persson 2013). For instance, equilibrium biomass (stage-specific and/or total biomass) can increase with mortality, which relaxes competition in the bottleneck stage. This phenomenon is called ‘biomass overcompensation’, and has implications for community dynamics and structure (Persson *et al.* 2007; de Roos *et al.* 2007; Ohlberger *et al.* 2011b). Ontogenetic asymmetry can emerge from differences in the allometric scaling of metabolic rate and ingestion (intrinsic properties) or through life stage-specific differences in food availability or mortality (extrinsic properties) (Persson & de Roos 2013; Reichstein *et al.* 2015). However, temperature dependence of biological rates as a source of ontogenetic asymmetry has hitherto been overlooked. In fact, our understanding of how increasing temperature affects animal populations is almost exclusively limited to scenarios assuming no size dependence in either performance or temperature effects (but see Ohlberger *et al.* 2011a). Under such assumptions, the size distribution does not influence the dynamics of the population, which constitutes a limiting case in animal populations (Persson & de Roos 2013). Therefore, a general theory on population responses to rising temperatures acknowledging the ontogenetic asymmetry of animal populations is lacking, despite the ubiquity of intraspecific variation in both body size and temperature dependence.

We fill this knowledge gap on how temperature affects population regulation by accounting for observed interactive effects of temperature and mass on fundamental biological rates in a dynamical model. The model is a temperature-dependent, stage-structured consumer-resource model, parameterised using experimental data on metabolic and foraging rates of a zooplanktivorous freshwater fish species. In addition, we collate a data set on intraspecific scaling in teleost fishes and demonstrate that temperature-dependent allometry is common. We find that size-specific temperature scaling of vital rates can generate stage-specific and total population responses to warming that are drastically different from when assuming independent effects of body size and temperature, including shifts in population regulation, community structure and responses to mortality.

MATERIAL AND METHODS

We extend a stage-structured biomass model to incorporate interactive effects of mass and temperature on vital rates to study consumer-resource responses to warming. Stage-structured biomass models (de Roos *et al.* 2008) are bioenergetic

models derived from more complex physiologically structured population models (Metz & Diekmann 1986; de Roos *et al.* 1992), founded in dynamic energy budget theory. Both modelling frameworks mechanistically link individual-level rates such as growth, which depends on size- or mass dependent consumption and metabolism, to population dynamics (de Roos *et al.* 2008).

Mass- and temperature-dependence of individual-level rates

To account for temperature dependence in the stage-structured biomass models, we extend the general mass- and temperature-dependence equation of the MTE (see equation in ‘Introduction’) to include a linear temperature dependence of the allometric exponent (see Ohlberger *et al.* 2012). The generic equation for allometric and temperature-dependent rate Y is thus formulated as $Y = Y_0(T_0)m^{b'+c_Y(T-T_0)}e^{E(T-T_0)/kTT_0}$, where T is temperature, Y_0 is the normalisation constant, b' is the allometric exponent at the reference temperature (T_0), c_Y is a linear temperature dependence of the exponent and E is the activation energy (temperature sensitivity). Thus, c_Y captures the difference in the slope of the log-log relationship of the rate against mass for each unit temperature relative to T_0 . This is the key parameter, alongside temperature, that we vary in subsequent analyses, as it governs the strength and direction of the size- and temperature interaction for the scaling of rates.

We denote the term $e^{E(T-T_0)/kTT_0}$ as $r_Y(T)$, where Y refers to the individual-level rates that are temperature dependent (Fig. 1; see also the Appendix in Supporting Information). The function $r_Y(T)$ equals 1 at T_0 (19°C) for all rates. Thus, temperature dependence is added to allometric rates estimated at T_0 by multiplying the rate with $r_Y(T)$, and by adding $c_Y(T-T_0)$ to the allometric exponent (see Table 1). Parameters are primarily derived from controlled temperature experiments on roach (*Rutilus rutilus* Linnaeus, 1758) (see Appendix).

Dynamics of the stage-structured consumer–resource system

We use mass- and temperature-dependent individual-level rates (e.g. feeding, metabolism) to model a consumer–resource system consisting of a zooplanktivorous fish population with an immature juvenile stage (J) and a mature adult stage (A). We explicitly study intraspecific exploitative competition as these stages feed on a shared unstructured zooplankton resource (R), mimicking a typical system in which intraspecific interactions and ontogenetic asymmetry shape population dynamics.

The dynamics of the consumer stages and the resource, as functions of temperature- (T) and mass- (m) dependent rates, are given by the following ordinary differential equations describing changes in biomass density:

$$\frac{dR}{dt} = \delta[T](R_{max} - R) - I_J(R, T, m)J - I_A(R, T, m)A \quad (1)$$

$$\begin{aligned} \frac{dJ}{dt} = & v_A^+(R, T, m)A + v_J(R, T, m)J \\ & - \gamma[v_J^+(R, T, m)J - \mu_J(T, m)J \end{aligned} \quad (2)$$

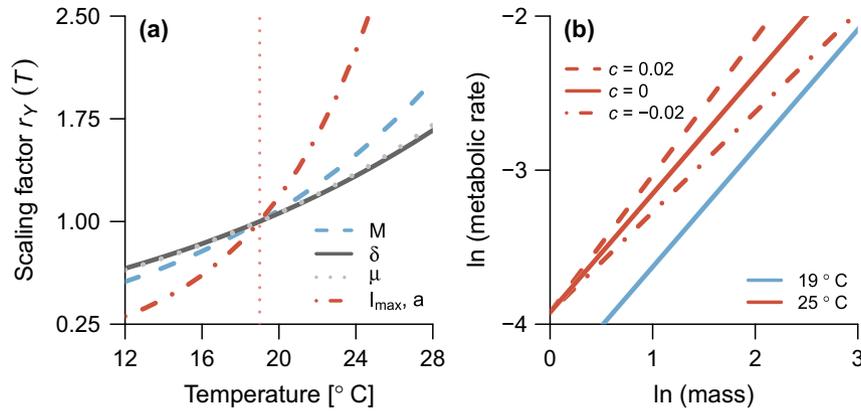


Figure 1 (a) Size-independent temperature functions for metabolic rate (M , blue dashed line), resource turnover rate (δ , dark grey line), background mortality (μ , grey dotted line) and functional response parameters (I_{max} and a , red dot- and dash line). Vertical red points indicate T_0 (19°C), where all temperature factors equal 1 and the temperature-dependent function collapses into the allometric function. (b) The combined effect of the temperature scaling factor and temperature-dependent allometry on metabolic rate over mass on the natural log scale, illustrated with two contrasting temperatures and three values of the c -parameters. When $c \neq 0$ (red dashed and dot- and dash lines), both the elevation and slope of the $\ln(\text{rate})$ - $\ln(\text{mass})$ plot change.

Table 1 Model functions used in the dynamic model

Function	Expression	Description
$I_i(R, T, m)$	$\frac{\eta_i(R, T, m)}{1 + \frac{\eta_i(R, T, m)}{I_{max, i}(T, m)}}$	Ingestion rate
$\eta_i(R, T, m)$	$a_i(T, m)R(T)^*$	Encounter rate
$a_i(T, m)$	$r_I(T)A \left(\frac{m_i}{m_{opt}} \exp\left(1 - \frac{m_i}{m_{opt}}\right) \right)^{\alpha' + c_I(T - T_0)}$	Attack rate
$I_{max, i}(T, m)$	$r_I(T)\varepsilon_1 m_i^{\beta_2' + c_I(T - T_0)}$	Maximum ingestion rate
$M_i(T, m)$	$r_M(T)\rho_1 m_i^{\beta_2' + c_M(T - T_0)}$	Metabolic rate
$v_i(R, T, m)$	$\sigma I_i(R, T, m) - M_i(T, m)$	Net-biomass production
$v_i^+(R, T, m)$	$\begin{cases} v_i(R, T, m) & \text{if } v_i(R, T, m) > 0 \\ 0 & \text{Otherwise} \end{cases}$	Net-biomass production limited to positive values
$\gamma(v_j^+(R, T, m))$	$\frac{v_j^+(R, T, m) - \mu_j(T, m)}{1 - z \frac{1 - \mu_j(T, m)}{v_j^+(R, T, m)}}$	Maturation rate
$\mu_i(T, m)$	$r_\mu(T)\phi_1 m_i^{\phi_2}$	Mortality rate

Note that subscript i refers to consumer life stage.

*When adults feed on their resource (R_A), i.e. when $p > 0$:
 $\eta_A = a_A(T, m)R(1 - p) + a_A(T, m)R_A p$

$$\frac{dA}{dt} = \gamma[v_j^+(R, T, m)]J + v_A(R, T, m)A - v_A^+(R, T, m)A - \mu_A(T, m)A \quad (3)$$

All individual-level rates are per unit biomass. Hence, rates at the level of the population are calculated by multiplying rates per unit biomass with the stage-specific biomass. The resource is assumed to grow according to semi-chemostat dynamics with temperature-dependent turnover rate $\delta(T)$ due to increased metabolic rate (Savage *et al.* 2004), reaching R_{max} in the absence of consumers. Semi-chemostat dynamics ensures that the model conforms to mass-conservation principles, since resource productivity does not scale with resource density as in the commonly assumed logistic growth equation (de Roos & Persson 2013). However, we also analysed the model, assuming

[Correction added on 18 January 2018, after first online publication: Table 1, Figures 1 and 5 have been updated]

logistic resource growth to confirm that our results were not limited to this assumption (Fig. S8 in the Appendix).

Ingestion rate, $I_i(R, T, m)$, follows a Holling type II functional response with size- and temperature-dependent maximum ingestion rate, $I_{max, i}(T, m)$ and attack rate $a_i(T, m)$ (Holling 1959), where the subscript i refers to the consumer life stage (juveniles [J] or adults [A]) (Table 1). The encounter rate, $\eta_i(R, T, m)$, is given by the product $a_i(T, m)R(T)$. For a given resource body size, $a_i(T, m)$ is assumed to be a hump-shaped function of consumer body size (Persson *et al.* 1998). Net biomass production, $v_i(R, T, m)$, as a function of the resource (R), temperature (T) and mass (m), is the difference between the product $\sigma I_i(R, T, m)$ and the metabolic costs $M_i(T, m)$, where σ is the assimilation efficiency. Reproduction and somatic growth only occurs when $v_i(R, T, m)$ is positive (denoted $v_i^+(R, T, m)$), in adults and juveniles respectively. If $v_i(R, T, m) < 0$, biomass of stage i is lost through starvation. We assume adults invest all surplus energy in reproduction, $v_A^+(R, T, m)$, and hence do not grow in size after reaching maturation ($s = s_m$), and that juveniles ($s < s_m$) invest all surplus net energy in somatic growth, $v_J^+(R, T, m)$. The maturation rate also depends on juvenile mortality, μ_J , and the newborn to adult size ratio, z , representing the size range over which juveniles need to grow before maturing into the adult stage (de Roos *et al.* 2008) (Appendix). A visual representation of the temperature-dependent stage-structured biomass model is presented in Fig. 2, and model functions are found in Table 1.

Model analyses

To investigate the effects of a temperature-dependent allometry of vital rates on the equilibrium dynamics of a stage-structured population, we vary the temperature- and mass interaction parameter of metabolic rate, c_M , while setting c_I , the interaction coefficient for functional response parameters, to 0. For simplicity, we henceforth refer to c_M as c , which captures the temperature effect of the metabolic scaling exponent relative to ingestion, and let it vary within a range comparable to published estimates (Ohlberger *et al.* 2012). Thus,

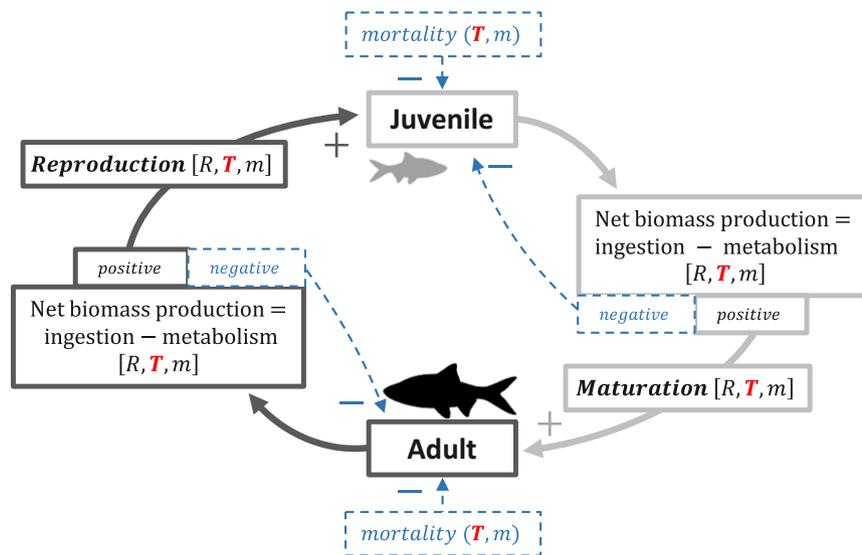


Figure 2 Flowchart of the stage-structured biomass model of a consumer population and its resource indicating temperature (T), mass (m), and resource (R) dependence of the consumer vital rates. This model mechanistically links individual-level rates such as maturation and reproduction, which are derived from temperature- and mass-dependent consumption and metabolism, to population dynamics at different temperatures. Temperature dependence is indicated with red and bold. Blue dashed lines indicate biomass losses (background mortality and starvation, the latter occurring when net biomass production is negative). Note that ingested energy is assimilated with a specific efficiency (σ), and that resource biomass (not illustrated) is directly affected by predation by consumers and temperature, such that the resource grows with a temperature-dependent turnover rate. For further details on model functions see ‘Material and Methods’ and Table 1, and for details about the parameterisation, using detailed experimental data, we refer to the Appendix.

positive c -values benefit smaller over larger individuals in warmer environments. It does not matter qualitatively which parameter is varied (c_M or c_I), as it is the relation between the allometric exponents of metabolic rate and ingestion that affects the size-dependent performance, given equal mortalities (de Roos & Persson 2013). In our model, background mortality rates are functions of size and temperature (Table 1). Because stage-specific background mortality is less influential for population regulation than stage-specific resource availability and scaling of ingestion and metabolic rate (Persson & de Roos 2013), most of the temperature effects are assumed to result from changes in the efficiency of biomass production.

To further generalise our results, we modelled a niche-broadening of adults by adding a resource (R_A) exclusive to the adults in addition to the resource shared with the juveniles. This allows us to assess how a warming-induced intrinsic and an extrinsic factor jointly shape population regulation. In these scenarios, adults feed on the exclusive resource R_A at a proportion p , and $1-p$ on the shared resource, R . By default we assumed equal productivities (R_{max}) of R and R_A (but see Appendix; Figs. S6–S7). We also performed sensitivity analyses on functional response and resource parameters, including above optimum temperature scenarios. This was modelled by assuming lower activation energy of feeding vs metabolic costs, which captures the mismatch due to the unimodal and exponential temperature dependence of ingestion and metabolism (Jobling 1997; Englund *et al.* 2011) respectively (Appendix).

We assess how temperature- and size-dependent scaling of metabolism affects population regulation under warming by tracking population-level maturation- and reproduction rates (and emerging juvenile or adult bottlenecks). To do this, we

perform continuations of stable equilibria as functions of temperature given different mass- and temperature scaling scenarios, using the MATLAB (MATLAB, 2014) package MATCONT (Dhooge *et al.* 2003).

Empirical analysis of temperature dependence of metabolic exponents

In order to assess the temperature dependence of the mass exponent of metabolic rate ($M[T, m]$) within species, we fitted the statistical model:

$$\ln M = \beta_0 + c_e T \times \ln(m) + \varepsilon, \quad (4)$$

where β_0 is the intercept and ε is the error term, to oxygen consumption data (proxy for metabolic rate, Brown *et al.* 2004) acquired from FishBase (www.fishbase.org, downloaded on 2017-03-14) (Froese & Pauly 2016). In this model, the c_e coefficient (subscript e refers to empirical) determines how much the slope of the log–log plot of metabolic rate and mass differs per unit temperature (Fig. 1b). Thus, c_e is equivalent to the parameter c in our dynamic model. We also fitted the model without c_e , resulting in one slope (b) per temperature and species combination (where b is equivalent to the allometric exponent of the MTE). Species were selected from the total pool of species in FishBase for which there is metabolic rate data ($n=332$) if the experiments allowed for estimation of the mass exponent for a suitable and comparable size range for three or more temperature treatments. We used only post-larvae experiments, and excluded all experiments with additional stressors applied (e.g. hypoxia and extreme temperatures), resulting in 20 species in the final analysis, spanning a mass range of 0.1 to 10400 g, and a temperature range of 3 to 35°C (Appendix). R version 3.3.2 (R Core Team, 2016) was used for statistical analysis.

RESULTS

Population responses to temperature

When temperature affects the size dependence ($c \neq 0$) of metabolic rate relative to ingestion, warming can shift the population regulation by altering the competitive dominance among individuals of different sizes (Fig. 3). This leads to a redistribution of biomass between life stages in the population with warming (Fig. 3a). In the absence of warming (at T_0 , 19°C), equilibrium biomass densities are identical in all scaling scenarios, and reproduction rate limits total population growth (here rate of change in equilibrium biomass density) (Fig. 3). This is evident by the higher population-level maturation than reproduction rate and by the biomass accumulation in the inferior (adult) stage. It is also indicative of competitive inferiority of the adult stage, as their net-biomass production per biomass is lower than that of juveniles. Temperature-induced shifts in regulation depend on how warming alters the size dependence of metabolic rate relative to that of ingestion. If the ratio of mass exponents of metabolic rate to ingestion decreases (if $c < 0$; Fig. 3a,d), such that the biomass production of the inferior adult stage (at the reference temperature T_0) benefits from warming relative to juveniles, both stages increase initially. Adult and total biomass decrease prior to the switch in regulation due to increased competition among juveniles, leading to a lower maturation rate. At 34.3°C, a shift in regulation occurs. Beyond this temperature population growth is limited by slow maturation (Fig. 3a,d). If the temperature dependence of metabolic allometry relative to ingestion instead is positive ($c > 0$), stage-specific and total biomass decline with temperature for most of the studied temperature range (Fig. 3c). This is due to a relative increase in the juvenile maturation rate, which leads to a build-up of biomass in the less efficient (bottleneck) adult stage (Fig. 3c,f). When temperature does not affect the size dependence of individual rates ($c = 0$), warming does not induce a shift in

population regulation, and the population remains relatively stable over temperature as well as reproduction limited over the whole temperature range (Fig. 3b,e). Moreover, temperature dependence of metabolic allometry mediates the hump-shaped overcompensatory response to increased mortality, as mortality relaxes energetic bottlenecks in the population (Fig. S1 in the Appendix).

Resource dynamics

The equilibrium resource density consistently decreases in all scaling scenarios with temperature (Fig. 3a,d), partly due to the higher temperature sensitivity of consumer feeding rate relative to resource turnover rate (compare with Fig. S3 in the Appendix). This decrease occurs irrespective of c , but is strongest when total consumer biomass increases with temperature. Stronger intraspecific competition in consumers due to declining resource density and an increased top down control in the food web thus appears to be a general response to increasing temperatures. Because the extent of the decline in resource biomass density is determined by consumer population density, which in turn is governed by c , the temperature dependence of consumer allometry also shapes the temperature response of the consumer-resource community (Fig. 3).

Generalising the model

As shifts in regulation induced by warming are caused by changes in the relative performance of differently sized consumers, the productivity of the shared resource (maximum biomass density, R_{max}) does not qualitatively change the results or conclusion (Fig. S2 in the Appendix). Similarly, the relative activation energies of ingestion and metabolism do not affect the role of c in shaping population regulation, as they do not influence the size-based competitive dominance (Figs S3–S5 in the Appendix). However, the ratio of the

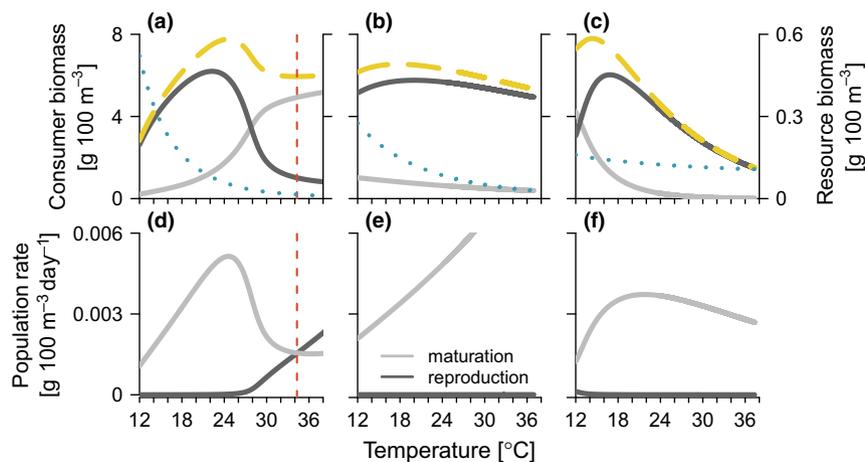


Figure 3 Biomass densities (top) and population level rates (reproduction/maturation) (bottom). Top row: equilibrium biomass density of juveniles (grey), adults (dark grey), total consumer biomass density (yellow dashed line, left y-axis) and resource biomass density (blue dotted line, right y-axis) as a function of temperature. Bottom row: total population rate of maturation- (grey) and reproduction (dark grey). Vertical dashed red lines show the points where the population exhibits ontogenetic symmetry (defined as equal maturation and reproduction rates in terms of biomass density per unit time). Panels (a) and (d) show model output assuming a negative temperature effect on the exponent of metabolism ($c = -0.02$), panels (b) and (e) correspond to temperature independent allometry ($c = 0$) and (c) and (f) show the model output with positive temperature dependence of the metabolic exponent ($c = 0.02$).

activation energies affects the ability to exert top down control of the resource by the consumer (Fig. S3 in the Appendix).

Moreover, warming can shift population regulation and stage-structure via temperature-dependent size scaling of biological rates even if the consumer life stages differ in prey use, e.g. when adults have a broader feeding niche than juveniles (Fig. 4). At $p=0.05$ (Fig. 4, middle panel), i.e. where adults spend 5% of their feeding on a resource R_A on which juveniles cannot feed, both intrinsic (temperature-dependent allometry of vital rates) and extrinsic (food availability) factors shape the mode of population regulation in warming environments. As feeding opportunity (p) of adults increases even further, intrinsic factors become less influential in shaping the mode of population regulation and stage-structure (though it still affects consumer biomass densities), and juveniles are dominant in terms of biomass for most of the c -temperature parameter space, except at cold temperatures ($<15^\circ\text{C}$) and negative c -values ($p=0.1$, Fig. 4, right panel). The same qualitative pattern emerges when varying the relative productivity of R_A ($x=0.5$) (Fig. S7 in the Appendix), with rising temperatures inducing shifts in population regulation. Assuming semi-chemostat resource dynamics over the commonly assumed logistic growth (see ‘Material and Methods’) does not influence our general conclusion about the role of c for temperature effects on population regulation (Fig. S7 in the Appendix).

Empirical analysis of temperature-dependent allometry

We identified significant interactions between mass and temperature for metabolic rate in 6 of the 20 species analysed, with effect sizes (c_e) ranging from -0.021 to 0.032 (Fig. 5b). Neither the effect size nor the likelihood of significance was related to the temperature range used in the experiments for each species (Fig. 5b). The distribution of metabolic rate exponents (b) estimated at single temperatures showed large variation around the commonly predicted value of 0.75 (Fig. 5a). Deviations from 0.75 are expected if the size scaling of metabolic rate depends on temperature and experiments have been performed under several temperatures. The realised b -values in our models (i.e. the allometric exponent at different temperatures given the c -parameter) are within the estimated distribution of empirical b -values (Fig. 5a, horizontal grey bar).

DISCUSSION

The effects of warming on population dynamics have with few exceptions been studied under the assumptions that both individual performance and temperature dependence of vital rates are independent of body size. However, size-dependent individual performance (ontogenetic asymmetry) is widespread in nature, and research suggests that temperature affects the interspecific allometric exponent of metabolic rate in a range of taxa (Glazier 2005, 2014). Here, we find support for temperature-dependent intraspecific allometry in metabolism, and analysed its consequences for population responses to rising temperatures. Our model analyses reveal that increasing temperatures can redistribute biomass between life stages and shift the mode of population regulation through temperature-dependent allometry alone, by altering the competitive dominance between consumer life stages. This shift causes changes in the community structure and altered responses to increased mortality. Our results are consistent for a range of assumptions regarding temperature scaling, consumer feeding niches, resource productivity and type of resource growth (Appendix). We therefore argue that this aspect of temperature scaling is important to recognise for predicting effects of increasing temperatures on populations and communities.

A large body of observational (Daufresne *et al.* 2009; Pauly 2010; Baudron *et al.* 2014) and experimental (Strong & Daborn 1980; Hoefnagel & Verberk 2015; Messmer *et al.* 2016) research show that temperature disproportionately affects large individuals, resulting in the widespread temperature-size rule (TSR) (Atkinson 1994; Ohlberger 2013). The TSR states that higher temperatures during ontogeny lead to faster growth and development but smaller adult body sizes (Atkinson 1994), and it has been linked to temperature effects on allometric exponents. Specifically, the TSR can be explained by optimal resource allocation if increasing temperature reduces the allometric exponent of ingestion relative to metabolic rate (Kozłowski *et al.* 2004). Such temperature-dependent size scaling of metabolism and maximum ingestion was found in our study species roach (Appendix), in the isopod *Idotea baltica* (Strong & Daborn 1980), and was also corroborated in Angilletta & Dunham (2003), which found a decrease in thermal optimum for growth efficiency. While more studies are needed to assess the generality of such scaling, and to derive quantitative

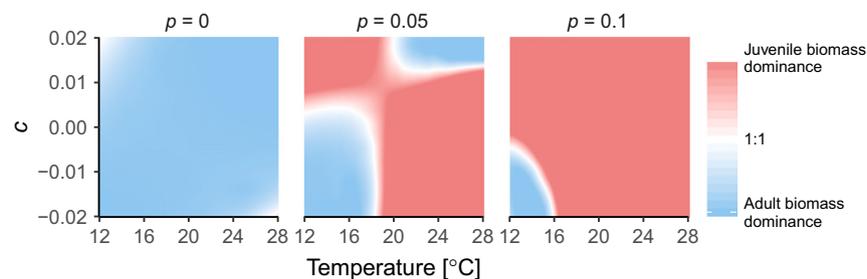


Figure 4 Contour plot of loess-smoothed juvenile to adult biomass ratio (indicative of mode of population regulation) as a function of temperature and the size dependence (c) of the temperature effect on the exponent of metabolism, given different proportions (p) with which adults feed on their exclusive resource R_A (which has equal productivity as R , i.e. the productivity scaling factor (x) equals 1). Blue colour indicates biomass dominance of the adult stage, red is biomass dominance of juveniles and white means equal biomass of adults and juveniles.

theories (Angilletta & Dunham 2003), it appears to be a common pattern. Importantly, it allows us to mechanistically model TSR-effects on population dynamics and size structure using allometric scaling of vital rates in a bioenergetic framework, rather than assuming a temperature dependence directly of e.g. body size.

A key conclusion in our study is that the overall response of a population to temperature is mediated by its size structure and intraspecific interactions. Therefore, to understand the general implications of size-dependent temperature effects, it is important to also assess which type of asymmetry and hence which mode of population regulation (i.e. regulated by slow maturation or reproduction) is more frequent in nature. At reference temperature, our model is consistent with other studies indicating that regulation through limited reproduction might be more common in freshwater fish populations (Byström *et al.* 1998; Ohlberger *et al.* 2011b; Persson & de Roos 2013; Schröder *et al.* 2014). This is also supported by empirical data showing that metabolic rate tends to increase faster with body mass than ingestion, i.e. a negative relationship between energetic efficiency and body size (Glazier 2005; Basset *et al.* 2012; but see Pawar *et al.* 2012). If temperature further enhances this negative relationship (e.g. by decreasing the ratio of ingestion vs metabolic exponents), and population regulation through limited reproduction is more common, our model suggests that total consumer biomass declines with increasing temperature. This is because a larger portion of the biomass is accumulated in the life stage less efficient in producing new biomass. Such redistribution of biomass could, as was the case in our study, affect the ability of consumers to exert top down control of the resource, which several studies predict to increase with temperature due to faster increase in feeding rates relative to resource growth (O'Connor 2009; Bruno *et al.* 2015). However, if consumer biomass declines due to temperature-dependent allometry, the ability to suppress the resource is reduced (Fig. 3c,f). In fact, this could cause a net increase in resource biomass density even when

the temperature sensitivity of resource turnover rate is similar to that of feeding (Fig. S3 in the Appendix). However, both regulation through maturation and reproduction have been observed empirically (Schröder *et al.* 2014), with the former likely being the result of a combination of extrinsic and intrinsic factors (de Roos & Persson 2013). Therefore, community responses to increasing temperatures can vary depending on how intraspecific interactions, which shape consumer size structure, are affected by temperature.

In our empirical data set, we found that six out of 20 species showed statistically significant interactive effects of size and temperature for metabolic rate, derived from experiments that were not specifically designed to test this interaction. This suggests that the general assumption of no mass-temperature interaction is invalid. Moreover, we found more negative than positive coefficients of a mass-temperature interaction on metabolism, i.e. temperature-induced increases in metabolic rate are less pronounced in larger size classes. However, the pattern is not as strong as in other studies of intra-specific scaling of metabolic rates made on single, or a smaller set of species than herein (Beamish 1964; Xie & Sun 1990; Glazier 2005; Ohlberger *et al.* 2012). We refrained from using data on published estimates in our analysis of allometric scaling in order to fit the same model to all species (Eqn. 4). Including literature data would shift the distribution of interaction coefficients further toward negative values, as they appear to be predominantly negative – see ‘Introduction’ for potential mechanisms (Beamish 1964; Xie & Sun 1990; Ohlberger *et al.* 2012; see also Killen *et al.* 2010 for a comparison across species). Future research should examine intraspecific scaling of vital rates (e.g. metabolic rate and ingestion) with respect to both temperature and mass for a broader range of taxa, and account for potential interactions between these factors.

The activation energy of ingestion is larger than for metabolic rate in our study species, in line with Vasseur & McCann (2005), but in contrast to Binzer *et al.* (2012). The ratio between these two rates, together with resource carrying

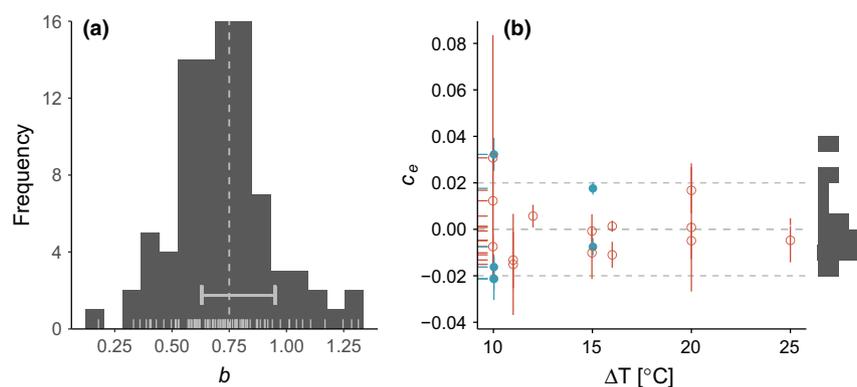


Figure 5 Results from estimation of the interaction between mass and temperature for the scaling of metabolic rate in 20 teleost fish species from experimental data. (a) Frequency distribution of metabolic scaling exponents (b) for each combination of species and temperature treatment ($n=90$). Vertical dashed grey line corresponds to the metabolic theory of ecology prediction of a $3/4$ exponent for metabolic rate. The horizontal grey line indicates the range of effective metabolic exponents used in the modelling analysis given the temperature range of 12–28°C. (b) Estimates of the interaction coefficient, c_e , governing the temperature dependence of the metabolic exponent within species (one estimate per species, $n=20$), plotted against the temperature range used for estimation. Vertical lines correspond to \pm one standard error. Blue, closed circles correspond to significant interaction terms at the 0.05 significance level ($n=6$ species) and red, open circles indicate non-significant interactions ($n=14$ species). Dashed horizontal lines indicate a c_e -value of zero and the maximum and minimum values of the parameter c in the dynamic models. The histogram shows the frequency distribution of c_e -values.

capacity, plays an important role for the stability of consumer resource systems at higher temperatures (Vasseur & McCann 2005; Binzer *et al.* 2012; Uszko *et al.* 2017). In our modelling framework, energetic efficiency over temperature is not solely a function of the activation energy of metabolic vs. feeding rate. Instead, it is a dynamic property that can be understood from interactive temperature- and size scaling of vital rates, mediated by intraspecific competition through size- and food-dependent individual performance. Thus, activation energy of metabolic rate relative to ingestion can determine if consumer biomass increases or decreases with rising temperatures, but does not influence population regulation or stability, which are governed by size-dependent processes (Fig. S3 in the Appendix).

To date, few studies have acknowledged temperature-dependent body size effects on vital rates and how they affect the dynamics and size structure of populations – despite empirical and theoretical support for both interactive size- and temperature effects and the importance of population size structure. Here we present empirical support for intraspecific temperature dependence of allometry in teleost fishes, and illustrate how this can induce shifts in population regulation and influence community structure in warmer environments. Specifically, if warming benefits the performance of the less competitive life-history stage such that the competitive dominance is shifted between stages within the population, rising temperatures induce shifts in the mode of population regulation. As population regulation is essential for understanding population and community dynamics, this study emphasises the importance of temperature-dependent allometry in size-structured populations for shaping population and community responses to climate warming.

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AUTHORSHIP

AG conceived the study. All authors contributed to the study design. ML and AG constructed and parameterised the model. ML performed modelling- and empirical analyses and wrote the first draft. All authors contributed substantially to the revision of the manuscript.

DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6nb35>

REFERENCES

- Angilletta, M.J. and Dunham, A.E. (2003). The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *Am. Nat.*, 162, 332–342.
- Atkinson, D. (1994). Temperature and organism size – a biological law for ectotherms? *Adv. Ecol. Res.*, 25, 1–58.
- Basset, A., Cozzoli, F. and Paparella, F. (2012). A unifying approach to allometric scaling of resource ingestion rates under limiting conditions. *Ecosphere*, 3, 1–14.
- Baudron, A.R., Needle, C.L., Rijnsdorp, A.D. and Marshall, C.T. (2014). Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change Biol.*, 20, 1023–1031.
- Beamish, F.W.H. (1964). Respiration of fishes with special emphasis on standard oxygen consumption: II. Influence of weight and temperature on respiration of several species. *Can. J. Zool./Rev. Can. Zool.*, 42, 177–188.
- Binzer, A., Guill, C., Brose, U. and Rall, B.C. (2012). The dynamics of food chains under climate change and nutrient enrichment. *Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci.*, 367, 2935–2944.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. and West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.
- Bruno, J.F., Carr, L.A. and O'Connor, M.I. (2015). Exploring the role of temperature in the ocean through metabolic scaling. *Ecology*, 96, 3126–3140.
- Byström, P. and Andersson, J. (2005). Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (Arctic char). *Oikos*, 110, 523–536.
- Byström, P., Persson, L. and Wahlström, E. (1998). Competing predators and prey: juvenile bottlenecks in whole-lake experiments. *Ecology*, 79, 2153–2167.
- Daufresne, M., Lengfellner, K. and Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proc. Natl Acad. Sci. USA*, 106, 12788–12793.
- Dhooge, A., Schellekens, T. and Kuznetsov, Y.A. (2003). MATCONT: a MATLAB package for numerical bifurcation analysis of ODEs. *ACM Trans. Math. Softw.*, 29, 141–164.
- Englund, G., Öhlund, G., Hein, C.L. and Diehl, S. (2011). Temperature dependence of the functional response. *Ecol. Lett.*, 14, 914–921.
- Froese, R. and Pauly, D. (Eds) (2016). FishBase. World Wide Web electronic publication. www.fishbase.org (10/2016).
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. and Charnov, E.L. (2001). Effects of size and temperature on metabolic rate. *Science*, 293, 2248–2251.
- Glazier, D.S. (2005). Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. *Biol. Rev. Camb. Philos. Soc.*, 80, 611–662.
- Glazier, D.S. (2010). A unifying explanation for diverse metabolic scaling in animals and plants. *Biol. Rev. Camb. Philos. Soc.*, 85, 111–138.
- Glazier, D.S. (2014). Scaling of metabolic scaling within physical limits. *Systems*, 2, 425–450.
- Hoefnagel, K.N. and Verberk, W.C. (2015). Is the temperature-size rule mediated by oxygen in aquatic ectotherms? *J. Therm. Biol.*, 54, 56–65.
- Holling, C.S. (1959). Some characteristics of simple types of predation and parasitism. *Can. Entomol.*, 91, 385–398.
- Jobling, M. (1997). Temperature and growth: modulation of growth rate via temperature change. In: *Global Warming: Implications for Freshwater and Marine Fish* (eds Wood, C.M. & McDonald, D.G.). Cambridge University Press, Cambridge, pp. 225–254.
- Killen, S.S., Atkinson, D. and Glazier, D.S. (2010). The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecol. Lett.*, 13, 184–193.
- Kozłowski, J., Czarnołęski, M. and Dańko, M. (2004). Can optimal resource allocation models explain why ectotherms grow larger in cold? *Integr. Comp. Biol.*, 44, 480–493.
- MATLAB (2014). version 8.4.0.150421 (2014b). The MathWorks Inc., Natick, MA.
- Messmer, V., Pratchett, M.S., Hoey, A.S., Tobin, A.J., Coker, D.J., Cooke, S.J. *et al.* (2016). Global warming may disproportionately affect

- larger adults in a predatory coral reef fish. *Global Change Biol.*, 23, 2230–2240.
- Metz, J.A.J. and Diekmann, O. (1986). *The Dynamics of Physiologically Structured Populations*. Springer-Verlag, Heidelberg, Germany.
- Newell, R.C. (1973). Factors affecting the respiration of intertidal invertebrates. *Am. Zool.*, 13, 513–528.
- O'Connor, M.I. (2009). Warming strengthens an herbivore-plant interaction. *Ecology*, 90, 388–398.
- Ohlberger, J. (2013). Climate warming and ectotherm body size – from individual physiology to community ecology. *Funct. Ecol.*, 27, 991–1001.
- Ohlberger, J., Edeline, E., Vollestad, L.A., Stenseth, N.C. and Claessen, D. (2011a). Temperature-driven regime shifts in the dynamics of size-structured populations. *Am. Nat.*, 177, 211–223.
- Ohlberger, J., Langangen, Ø., Edeline, E., Claessen, D., Winfield, I.J., Stenseth, N.C. *et al.* (2011b). Stage-specific biomass overcompensation by juveniles in response to increased adult mortality in a wild fish population. *Ecology*, 92, 2175–2182.
- Ohlberger, J., Mehner, T., Staaks, G. and Hölker, F. (2012). Intraspecific temperature dependence of the scaling of metabolic rate with body mass in fishes and its ecological implications. *Oikos*, 121, 245–251.
- Pauly, D. (2010). *Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Water-Breathing Animals*. International Ecology Institute Oldendorf, Luhe, Germany.
- Pawar, S., Dell, A.I. and Savage, V.M. (2012). Dimensionality of consumer search space drives trophic interaction strengths. *Nature*, 486, 485–489.
- Persson, L. and de Roos, A.M. (2013). Symmetry breaking in ecological systems through different energy efficiencies of juveniles and adults. *Ecology*, 94, 1487–1498.
- Persson, L., Leonardsson, K., de Roos, A.M., Gyllenberg, M. and Christensen, B. (1998). Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theor. Popul. Biol.*, 54, 270–293.
- Persson, L., Amundsen, P.-A., De Roos, A.M., Klemetsen, A., Knudsen, R. and Primicerio, R. (2007). Culling prey promotes predator recovery – alternative states in a whole-lake experiment. *Science*, 316, 1743–1746.
- R Core Team (2016). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org/>. Accessed date, January 1, 2017
- Reichstein, B., Persson, L. and De Roos, A.M. (2015). Ontogenetic asymmetry modulates population biomass production and response to harvest. *Nat. Commun.*, 6, 6441.
- de Roos, A.M. and Persson, L. (2013). *Population and Community Ecology of Ontogenetic Development*. Princeton University Press, Princeton, NJ.
- de Roos, A.M., Diekmann, O. and Metz, J.A.J. (1992). Studying the dynamics of structured population models: a versatile technique and its application to *Daphnia*. *Am. Nat.*, 139, 123–147.
- de Roos, A.M., Schellekens, T., van Kooten, T., van de Wolfshaar, K., Claessen, D. and Persson, L. (2007). Food-dependent growth leads to overcompensation in stage-specific biomass when mortality increases: the influence of maturation versus reproduction regulation. *Am. Nat.*, 170, E59–E76.
- de Roos, A.M., Schellekens, T., van Kooten, T., van De Wolfshaar, K., Claessen, D. and Persson, L. (2008). Simplifying a physiologically structured population model to a stage-structured biomass model. *Theor. Popul. Biol.*, 73, 47–62.
- Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. and Charnov, E.L. (2004). Effects of body size and temperature on population growth. *Am. Nat.*, 163, 429–441.
- Schröder, A., van Leeuwen, A. and Cameron, T.C. (2014). When less is more: positive population-level effects of mortality. *Trends Ecol. Evol.*, 29, 614–624.
- Strong, K.W. and Daborn, G.R. (1980). The influence of temperature on energy budget variables, body size, and seasonal occurrence of the isopod *Idotea baltica* (Pallas). *Can. J. Zool./Rev. Can. Zool.*, 58, 1992–1996.
- Uszko, W., Diehl, S., Englund, G. and Amarasekare, P. (2017). Effects of warming on predator–prey interactions: a resource-based approach and a theoretical synthesis. *Ecol. Lett.*, 20, 513–523.
- Vasseur, D.A. and McCann, K.S. (2005). A mechanistic approach for modelling temperature-dependent consumer-resource dynamics. *Am. Nat.*, 166, 184–198.
- Verberk, W.C.E.P. and Atkinson, D. (2013). Why polar gigantism and Palaeozoic gigantism are not equivalent: effects of oxygen and temperature on the body size of ectotherms. *Funct. Ecol.*, 27, 1275–1285.
- West, G.B., Brown, J.H. and Enquist, B.J. (1997). A general model for the origin of allometric scaling laws in biology. *Science*, 276, 122–126.
- West, G.B., Brown, J.H. and Enquist, B.J. (1999). The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science*, 284, 1677–1679.
- Xie, X. and Sun, R. (1990). The bioenergetics of the Southern Catfish (*Silurus meridionalis* Chen). I. resting metabolic rate as a function of body weight and temperature. *Physiol. Zool.*, 63, 1181–1195.

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