Will Invertebrates Require Increasingly Carbon-Rich Food in a Warming World?

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ABSTRACT: Elevated temperature causes metabolism and respiration to increase in poikilothermic organisms. We hypothesized that invertebrate consumers will therefore require increasingly carbon-rich diets in a warming environment because the increased energetic demands are primarily met using compounds rich in carbon, that is, carbohydrates and lipids. Here, we test this hypothesis using a new stoichiometric model that has carbon (C) and nitrogen (N) as currencies. Model predictions did not support the hypothesis, indicating instead that the nutritional requirements of invertebrates, at least in terms of food quality expressed as C:N ratio, may change little, if at all, at elevated temperature. Two factors contribute to this conclusion. First, invertebrates facing limitation by nutrient elements such as N have, by default, excess C in their food that can be used to meet the increased demand for energy in a warming environment, without recourse to extra dietary C. Second, increased feeding at elevated temperature compensates for the extra demands of metabolism to the extent that, when metabolism and intake scale equally with temperature (have the same Q_{10}), the relative requirement for dietary C and N remains unaltered. Our analysis demonstrates that future climate-driven increases in the C:N ratios of autotroph biomass will likely exacerbate the stoichiometric mismatch between nutrient-limited invertebrate grazers and their food, with important consequences for C sequestration and nutrient cycling in ecosystems.

Keywords: temperature, food quality, threshold elemental ratio, growth efficiency, metabolism, ingestion.

Introduction

The surface temperature of the earth increased by about 0.6°C during the twentieth century and may increase by a further 1.0°–3.7°C by the year 2100, depending on future greenhouse gas emissions (IPCC 2013). Embedded within this gradual change are strong regional and temporal variations in temperature on a range of scales, including extreme events. Temperature governs biochemical reaction kinetics and, thereby, many physiological processes in organisms (Gillooly et al. 2001). Poikilothermic invertebrates are especially vulnerable to warming via impacts on growth, reproduction, foraging, immune competence, and competitiveness (Pörtner and Farrell 2008). In particular, elevated temperature gives rise to increased metabolism and respiration (Gillooly et al. 2001; Angilletta et al. 2004; Ehnes et al. 2011; Ikeda 2014). Temperature thereby impacts on trophic interactions between consumers and prey (Rall et al. 2010; Dell et al. 2014) and, in turn, food-web dynamics and the structure and functioning of ecosystems (Walther et al. 2002; Friberg et al. 2009; Traill et al. 2010). Even relatively moderate warming could generate a cascade of trophic interactions (Barton and Schmitz 2009).

Invertebrates primarily use compounds rich in carbon (C) such as carbohydrates and lipids to meet the demands of metabolism, thereby sparing protein for growth and reproduction (Lemcke and Lampert 1975; Roman 1983; Elendt 1989). The energetic demands of respiration usually account for a major fraction of the organic matter processed by organisms (Mayor et al. 2009), in which case growth efficiency declines as respiration increases with temperature (Iguchi and Ikeda 1995; Heilmayer et al. 2004; Doi et al. 2010; Vucic-Pestic et al. 2011; Lemoine and Burkepile 2012; Cross et al. 2015). Animals should then require extra C in their diet (Acheampong et al. 2014) and may, accordingly, select for increasingly C-rich foods in a warming environment. Boersma et al. (2016), for example, found that when the marine copepod *Temora longicornis* was fed a mixture of the algal species *Rhodomonas salina* (with C:N:P of 320:38:1) and the heterotrophic dinoflagellate *Oxyrrhis marina* (C:N:P of 175:25:1), the zooplankter selected for the algal (high C) diet when exposed to elevated temperatures rather than for heterotrophic (low C) prey. Likewise, experimental work has shown that caterpillars increase their preference for carbohydrate-rich diets at high

temperatures when fed diets with differing carbohydrate-to-protein ratios (Lee and Roh 2010; Lee et al. 2015). It could also be the case that homeotherms prefer to eat food items with a relatively high C∶N because they have greater requirements for C in metabolism than poikilotherms (Klaassen and Nolet 2008).

Nutrient elements such as nitrogen (N) also play an important role in metabolism (Mayor et al. 2011; Zhu et al. 2016) and are likewise influenced by environmental temperature (Ikeda 2014). Protein turnover rates, for example, can reach 0.1 day^{-1} (Mente et al. 2002; Mayor et al. 2011). In contrast to the works described above, some studies have shown various insects selecting for diets that are rich in N (rather than C) at elevated temperatures. Lemoine et al. (2013), for example, found that the herbivorous beetle *Popillia japonica* selected for high-N plants when exposed to warming, suggesting increased limitation by N, when provided with a choice of nine plant species. In a similar fashion, Schmitz et al. (2016) noted that juvenile grasshoppers favored greater protein intake at elevated temperatures when fed diets with contrasting carbohydrate-to-protein ratios.

Growth is fueled via metabolism (West et al. 2001; Zuo et al. 2010), and so, in accordance with both the metabolic theory of ecology (Gillooly et al. 2001; Brown et al. 2004; Irlich et al. 2009) and Dynamic Energy Budget Models (Freitas et al. 2010; Teal et al. 2012; Kearney et al. 2013), the growth rate of a variety of organisms is seen to increase with increasing temperature (Gresens 1997; Campbell et al. 2001; Sogard and Olla 2001; Kendrick and Bernard 2013; Hayes et al. 2015; Yang et al. 2016). Greater intake rates are frequently seen at higher temperatures (Deason 1981; Durbin and Durbin 1992; Almeda et al. 2010; Yang et al. 2016) in response to the extra demand for substrates, without which additional growth cannot occur (Hayes et al. 2015). Given the multiple effects of temperature on metabolism, growth, and intake, the combined impact on the nutritional requirements for C and N in consumers is complex and not well understood (Makino et al. 2011; Persson et al. 2011; Kearney et al. 2013; Lemoine et al. 2013; Lee et al. 2015), especially as many invertebrates, including zooplankton and insects, are limited by nutrient elements (Hessen 1992; DeMott et al. 2001; Frost and Elser 2002; Huberty and Denno 2006). Understanding the effect of temperature on invertebrate nutrition requires a stoichiometric approach based on rules that define how organisms simultaneously process multiple elements in their food for metabolism and growth, taking into account both food quality and quantity. Although a large number of publications on organism stoichiometry have appeared over the past two decades, as have a wealth of papers on the potential consequences of rising temperatures for metabolism and growth, the combined effect of temperature and nutritional demands has received less attention (Persson et al. 2011; Boersma et al. 2016; Malzahn et al. 2016; Zhang et al. 2016).

Here, we present a new, relatively simple stoichiometric model to explore the interaction between temperature (including effects on both metabolism and intake) and food quality (expressed as C∶N ratio) on poikilothermic invertebrates. We focus on N as the nutrient element because it is typically limiting in terrestrial and marine environments, and therefore sufficient data are available for model parametrization. Specifically, we test the following hypothesis: Invertebrate consumers will require increasingly C-rich diets in a warming environment because the temperature-driven increase in the metabolic demand for C is proportionally greater than the demand for nutrient elements. A corollary to the hypothesis is that, if confirmed, consumers should preferentially select for increasingly C-rich foods in response to climate warming. Although our analysis is relevant for poikilothermic invertebrates in general, we focus on zooplankton because of their biogeochemical significance in aquatic ecosystems and the relative ease with which data can be obtained for both marine and freshwater species, facilitating parameterization of the model.

Model Description

The model presented herein has as its basis the fundamental principles of ecological stoichiometry as described by Anderson and Hessen (1995), but with new equations for metabolism (explicitly separating protein turnover and the energetic demands of respiration) and its dependence on temperature. The temperature dependence of food intake is also included. The model is parameterized for zooplankton but is constructed to represent poikilothermic invertebrates in general. Consumers are assumed to have fixed body composition. While absolute homeostasis is a simplification even for invertebrates, variations are considered to be minor relative to the flexible stoichiometry of autotrophs (Sterner and Elser 2002). Moreover, variations in the C∶N ratio in animals (our focus here) are much smaller than those in the C∶P ratio (Andersen and Hessen 1991; Sterner and Elser 2002).

Fundamentals of Stoichiometry

The basic principles of the stoichiometry of consumer growth, as presented in Anderson and Hessen (1995), are presented in this section, before proceeding to a description of the new model in the next. The equation for the growth, G (day^{-1}), of a zooplankter with C∶N ratio θ_Z experiencing food with C∶N ratio θ_f is

$$G = \beta_C k_C I_C = \beta_N k_N I_N \theta_Z \tag{1}$$

(Anderson and Hessen 1995), where I_C is ingestion of C (day^{-1}), I_N is ingestion in N units ($I_N = I_C/\theta_f$; mol N mol C^{-1} day^{-1}), β_C and β_N are absorption efficiencies (AEs) for C and N, re-

spectively (the efficiency of passing substrates across the gut wall; Penry 1998), and k_C and k_N are the corresponding net production efficiencies (NPEs; the fraction of absorbed substrates incorporated into new biomass). Imbalances between the demands of growth and metabolism and food C : N lead to either C or N limiting production (defined as the synthesis of new biomass, including reproduction), requiring disposal of the (nonlimiting) element in excess in order to maintain homeostasis. The simplest assumption is to fix the AEs, β_C and β_N, as constants, thereby assuming that stoichiometric regulation of homeostasis is primarily postabsorption by the gut (Anderson et al. 2005; Schoo et al. 2013). Net production efficiencies, k_C and k_N, are then variable, depending not only on utilization of substrates for growth and metabolism but also on the dissipation of excess C or N by respiration or excretion. Limiting elements are used for growth with maximum efficiency (no stoichiometric excess); these maximum NPEs for C and N are denoted k_C^* and k_N^*. The threshold elemental ratio (TER; θ_f^*) is the C : N ratio in food that exactly matches the requirements for growth and metabolism of the consumer, with neither C nor N being in excess. The equation for the TER is derived by rearranging equation (1), replacing I_N with I_C/θ_f:

$$\theta_f^* = \frac{\beta_N k_N^* \theta_z}{\beta_C k_C^*}. \tag{2}$$

The use of a fixed value to represent the maximum NPE for C, k_C^*, is simplistic because it takes no account of different terms in the metabolic budget nor of dependency on food quantity. When food is scarce, for example, k_C^* tends to be low because respiration accounts for a large proportion of the C budget (Urabe and Watanabe 1991). A number of stoichiometric models have been developed that explicitly represent basal metabolism in order to redress this difficulty (Anderson and Hessen 2005; Anderson et al. 2005; Acheampong et al. 2012). These models follow a sequence of steps when dealing with the fate of ingested substrates: intake, absorption, and basal metabolism, with remaining substrates used for growth and leftovers disposed of by respiration or excretion.

Model Equations

The new model presented here (fig. 1) has C and N as currencies and includes basal (resting) metabolism represented by two terms: biomass turnover (akin to protein turnover; parameter τ, day^{-1}; requiring both C and N in ratio θ_z) and other basal metabolism (parameter ζ, day^{-1}; a C-only cost representing basic cellular processes including production of adenosine triphosphate [ATP], maintenance of ionic and molecular gradients, etc.; Karr et al. 2012). The model also includes the energetic costs of acquiring food (including search-

ing for and capturing prey), ingestion, digestion, absorption, and assimilation. These costs are correlated with intake and are known collectively as specific dynamic action (SDA; parameter η), which is the ratio of C lost to respiration as a fraction of intake (Secor 2009).

The model equations are novel in three aspects: (i) growth and basal metabolism are calculated simultaneously (as they would occur in reality) rather than in a series, (ii) the synthesis of new biomass (G) and replacement biomass (τ) are treated biochemically as one and the same process, and (iii) the temperature dependence of metabolic processes, as well as ingestion, is included. A list of model variables and parameters is provided in tables 1 and 2. Based on i and ii above, the total synthesis of biomass, S_{tot} (the sum of G and τ; day^{-1}), can be calculated in analogous fashion to equation (1):

$$S_{tot} = G + \tau = \beta_C \kappa_C I_C = \beta_N \kappa_N I_N \theta_z. \tag{3}$$

Growth is then

$$G = \beta_C \kappa_C I_C - \tau = \beta_N \kappa_N I_N \theta_z - \tau. \tag{4}$$

Note that, in comparison to equation (1), parameters k_C and k_N have been replaced by parameters κ_C and κ_N (net synthesis efficiencies [NSEs]: the fraction of absorption allocated to S_{tot}). As with Anderson and Hessen (1995), C-rich compounds are preferentially used for respiration, thereby sparing protein (N) for growth (Roman 1983; Elendt 1989). The theoretical maximum NSE for N, κ_N^*, then equals 1.0. On the other hand, the maximum NSE for C, κ_C^*, is necessarily less than 1.0 because of both the energetic costs of SDA (parameter η) and other basal metabolic costs (parameter ζ). When C is limiting (no excess C), S_{tot} is $\beta_C I_C - \zeta - \eta I_C$, in which case κ_C^* is

$$\kappa_C^* = 1 - \frac{\zeta}{\beta_C I_C} - \frac{\eta}{\beta_C}. \tag{5}$$

By replacing κ_C and κ_N with κ_C^* and κ_N^* in either equation (3) or equation (4) and rearranging to solve for θ_f (with $I_N = I_C/\theta_f$), the TER is

$$\theta_f^* = \frac{\beta_N \kappa_N^* \theta_z}{\beta_C \kappa_C^*} = \frac{\beta_N \kappa_N^* \theta_z}{\beta_C - \zeta/I_C - \eta}. \tag{6}$$

Note that because the synthesis of new biomass and replacement biomass is considered a single process, subject to a single set of stoichiometric constraints, parameter τ does not appear in equations (5) and (6). This novel feature of the model simplifies the analysis in that the ideal food C : N—that is, the calculated TER—is not a direct function of biomass turnover, τ (note that there is, however, an indirect ef-
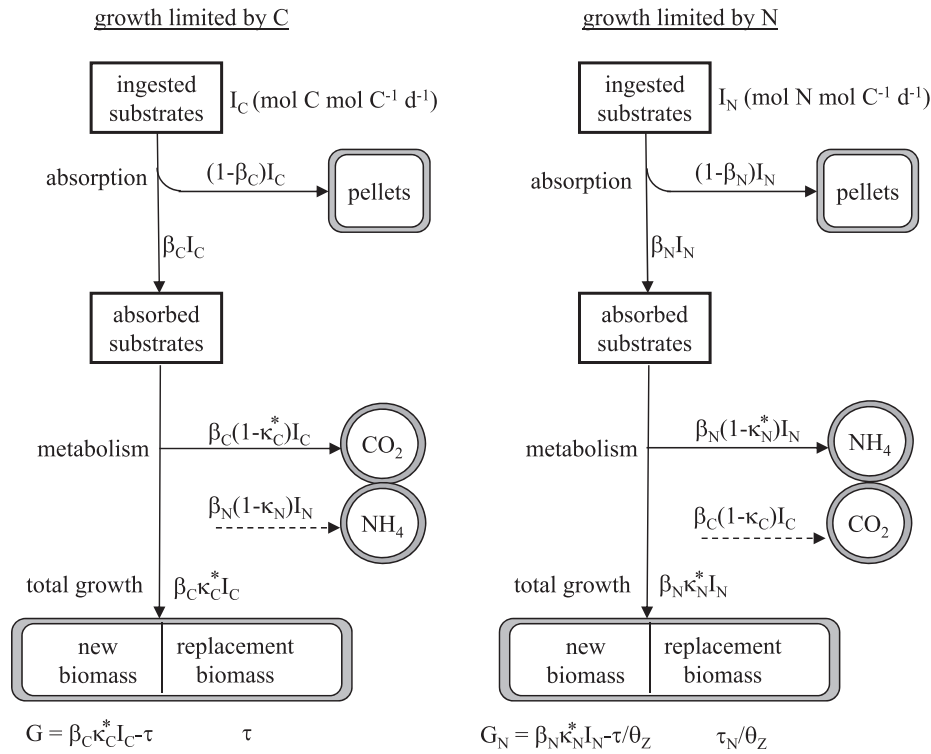
Figure 1: Flow pathways of carbon (C) and nitrogen (N) in the model, showing the separate cases for C versus N limitation. Note that nitrogen growth (G_N) and nitrogen biomass turnover (τ_N) are equivalent to G and τ, except with units of mol N mol C^{-1} day^{-1}. See tables 1, 2 for definitions of terms.

fect: increasing τ requires higher I_C in order to meet the costs of maintenance, driving the TER downward). The net utilization efficiencies, parameters κ_C and κ_N, depend on whether C or N is limiting:

$$\text{C limitation } (\theta_f < \theta_f^*): \kappa_C = \kappa_C^*, \ \kappa_N = \frac{\beta_C \kappa_C^* \theta_f}{\beta_N \theta_Z}, \quad (7)$$

$$\text{N limitation } (\theta_f > \theta_f^*): \kappa_C = \frac{\beta_N \kappa_N^* \theta_Z}{\beta_C \theta_f}, \ \kappa_N = \kappa_N^*. \quad (8)$$

C and N are lost via respiration and excretion, directly via metabolism, and as a means of alleviating stoichiometric excess. Losses due to biomass turnover are allocated as additional fluxes contributing to respiration (R, mol C mol C^{-1} day^{-1}) and excretion (E, mol N mol C^{-1} day^{-1}):

$$R = \beta_C(1 - \kappa_C)I_C + \tau, \quad (9)$$

$$E = \beta_N(1 - \kappa_N)I_N + \frac{\tau}{\theta_Z}. \quad (10)$$

Losses to fecal pellets, W_C and W_N, are

$$W_C = (1 - \beta_C)I_C, \quad (11)$$

$$W_N = (1 - \beta_N)I_N. \quad (12)$$

Zooplankton require minimum rations of C and N in order to meet the costs of metabolism ($\tau + \zeta$). The minimum C ration, $I_{\min C}$, occurs when $\beta_C \kappa_C^* I_C - \tau = 0$, in which case

$$I_{\min C} = \frac{\tau + \zeta}{\beta_C - \eta}. \quad (13)$$

Likewise, the minimum N ration, $I_{\min N}$, occurs when $\beta_N \kappa_N^* I_N - \tau/\theta_Z = 0$, giving

$$I_{\min N} = \frac{\tau}{\beta_N \kappa_N^* \theta_Z}. \quad (14)$$

The C:N of the minimum ration, $I_{\min C:N}$, is then

$$I_{\min C:N} = \frac{I_{\min C}}{I_{\min N}} = \frac{\beta_N \kappa_N^* \theta_Z}{\beta_C - \eta}\left(1 + \frac{\zeta}{\tau}\right). \quad (15)$$

Intake as a function of food concentration, F (mmol C m^{-3}), is described using a type III functional response (Holling 1959; Almeda et al. 2010):

$$I_C = \frac{I_{\max}F^2}{I_{\text{half}}^2 + F^2}, \quad (16)$$

Table 1: Model variables

Variable	Definition	Unit of measure
I_C	Intake: carbon	mol C mol C^{-1} day^{-1}
I_N	Intake: nitrogen	mol N mol C^{-1} day^{-1}
F	Food density	mmol C m^{-3}
G	Growth	Day^{-1}
S_{tot}	Total biomass synthesis	Day^{-1}
R	Respiration	mol C mol C^{-1} day^{-1}
E	Excretion	mol N mol C^{-1} day^{-1}
W_C	Fecal production: carbon	mol C mol C^{-1} day^{-1}
W_N	Fecal production: nitrogen	mol N mol C^{-1} day^{-1}
θ_f	Food carbon : nitrogen	mol C mol N^{-1}
θ_f^*	Threshold elemental ratio	mol C mol N^{-1}
θ_G	Growth carbon : nitrogen requirement	mol C mol N^{-1}
θ_M	Metabolism carbon : nitrogen requirement	mol C mol N^{-1}
κ_C^*	Maximum net synthesis efficiency: carbon	Dimensionless
κ_C	Realized net synthesis efficiency: carbon	Dimensionless
κ_N	Realized net synthesis efficiency: nitrogen	Dimensionless
$I_{min\,C}$	Minimum ration: carbon	mol C mol C^{-1} day^{-1}
$I_{min\,N}$	Minimum ration: nitrogen	mol N mol C^{-1} day^{-1}
$I_{min\,C:N}$	Carbon : nitrogen of minimum ration	mol C mol N^{-1}
T	Temperature	°C

where I_{max} is the maximum intake rate (mol C mol C^{-1} day^{-1}) and I_{half} is the half-saturation constant (mmol C m^{-3}).

The influence of temperature is included in the model by applying temperature quotient (Q_{10}) relationships to metabolism and intake, parameters Q_τ, Q_ζ, and Q_{IC} representing the temperature dependence of biomass turnover, other basal costs, and the maximum intake rate (parameters τ, ζ, and I_{max}, respectively). It may be reasonably assumed that the energy requirements associated with SDA (parameter η) are fixed and independent of temperature (Secor et al. 2007), although the experimental evidence is somewhat equivocal (Secor 2009). We adopt a parsimonious approach in this regard and assume that SDA is fixed; the findings and conclusions presented herein are not sensitive to this assumption.

Parameterization

The model is constructed for poikilothermic invertebrates in general, but is parameterized for marine copepods, a group of zooplankton that is ubiquitous throughout the global ocean. An advantage of the model is that it has only seven stoichiometric parameters (β_N, β_C, θ_Z, κ_N^*, τ, ζ, η), plus the extra parameters for temperature dependence (Q_τ, Q_ζ, Q_{IC}) and the functional response (I_{max}, I_{half}). The absorption efficiencies for C and N were assigned fixed values, $\beta_C = 0.64$ and $\beta_N = 0.69$ (Anderson 1994). Zooplankton C : N was set at $\theta_Z = 5.5$ mol C mol N^{-1} (e.g., Gismervik 1997). Parameter κ_N^*, the maximum net synthesis efficiency for N, could be assigned a value of 1.0, which gives the potential for 100%

Table 2: Model parameters

Parameter	Definition	Default value	Unit of measure
β_C	Absorption efficiency: carbon	.64	Dimensionless
β_N	Absorption efficiency: nitrogen	.69	Dimensionless
κ_N^*	Maximum net synthesis efficiency: nitrogen	.9	Dimensionless
τ	Biomass turnover	.094	Day^{-1}
ζ	Other basal costs	.052	Day^{-1}
η	Specific dynamic action	.12	Dimensionless
θ_Z	Consumer carbon : nitrogen	5.5	mol C mol N^{-1}
I_{max}	Maximum ingestion rate	1.3	mol C mol C^{-1} day^{-1}
I_{half}	Half saturation for intake	3.0	mmol C m^{-3}
Q_τ	Q_{10} for parameter τ	2	Dimensionless
Q_ζ	Q_{10} for parameter ζ	2	Dimensionless
Q_{IC}	Q_{10} for parameter I_{max}	2	Dimensionless

Note: Values for τ, ζ, and I_{max} are for a reference temperature of 17°C.

protein sparing. In reality, however, sparing is unlikely to reach 100% because the associated enzymatic pathway for generating energy using proteins will likely be downregulated, rather than totally excluded, in the presence of C-rich substrates; a value of $\kappa_N^* = 0.9$ was therefore used (e.g., Kuijper et al. 2004). Biomass turnover and other basal costs of metabolism were set at $\tau = 0.094$ day^{-1} (Anderson et al. 2005; based on measured excretion rates of *Daphnia* [DeMott et al. 1998]) and $\zeta = 0.052$ day^{-1} (Anderson et al. 2005), with both τ and ζ assigned a Q_{10} of 2 for temperature dependence ($Q_\tau = Q_\zeta = 2.0$; Ikeda et al. 2001). Specific dynamic action, parameter η, was assigned a value of 0.12 (Thor et al. 2002), meaning that 12% of intake is required to meet the associated bioenergetic costs. Parameter settings for the zooplankton functional response were $I_{max} = 1.3$ mol C mol C^{-1} day^{-1} (Kiørboe 1989) and $I_{half} = 3$ mmol C m^{-3} (Anderson et al. 2010), with a Q_{10} for intake, Q_{IC}, of 2 (Kiørboe et al. 1982; Durbin and Durbin 1992; Julian et al. 2001; Almeda et al. 2010). The values assigned to temperature-dependent parameters (τ, ζ, I_{max}) are all for a reference temperature of 17°C, which is the temperature used in the experiments of Kiørboe (1989) that are used as a basis for model-data intercomparison.

Results

A validation exercise was performed initially in order to demonstrate model performance with respect to fundamental concepts of how consumer growth is affected by (i) food quality and (ii) temperature-dependent intake (food quantity). The key hypothesis—namely, that consumers will require increasingly C-rich diets in a warming environment—was then examined in two stages. First, the model was used to investigate the effect of increasing metabolism at elevated temperatures on consumer nutritional requirements for C and N, without including the effect of temperature on intake. Second, the analysis was extended to include the effect of temperature on both metabolism and intake, providing an investigation of the degree to which increased intake associated with warming can offset (compensate for) the increasing costs of metabolism.

A key premise underscoring the hypothesis that animals should require increasingly C-rich diets with warming is that the C:N ratio of metabolism is higher than that of growth, with energetic costs being preferentially met using carbohydrates and lipids. Before proceeding further, we confirmed this assumption based on the model parameterization. The C:N ratio of metabolism (θ_M) is equal to the food requirement at the minimum ration—that is, the ration that exactly balances the costs of metabolism—with zero growth (eq. [15]). Using default parameter values (table 2), $\theta_M = 10.2$ mol C (mol N)$^{-1}$. Note that if the two components of metabolism, biomass turnover (τ) and other basal costs (ζ), scale equally with temperature—that is, have the same Q_{10}—then θ_M is

constant, independent of temperature. The C:N of growth (θ_G) is not simply the C:N ratio of the consumer but also includes C and N losses associated with absorption and SDA. Carbon growth efficiency when metabolism is zero ($\tau = \xi = 0$) is $\beta_C(1 - \eta/\beta_C)$ (eq. [5]), in which case each unit of growth requires $1/(\beta_C - \eta)$ units of C. The corresponding requirement for N is $1/(\beta_N\kappa_N^*)$, and so θ_G is calculated as

$$\theta_G = \frac{\beta_N\kappa_N^*\theta_Z}{\beta_C - \eta}. \tag{17}$$

Using default parameter values, $\theta_G = 6.6$ mol C (mol N)$^{-1}$. The premise that metabolism has a greater C:N than growth is thus supported ($\theta_G = 6.6 \ll \theta_M = 10.2$). Note that the ratio θ_M/θ_G is equal to $1 + \zeta/\tau$ (compare eq. [15] with eq. [17]), highlighting the importance of parameter ζ (other basal costs) in the analysis (if $\zeta = 0$, θ_G and θ_M would both equal 6.6). The optimal diet of consumers (which occurs at the TER) combines C and N as required in ratios θ_M and θ_G. The fraction of carbon intake used to meet the costs of metabolism, f, is

$$f = \frac{\tau + \zeta}{(\beta_C - \eta)I_C}. \tag{18}$$

The equation for the TER can then be recast as

$$\theta_f^* = \frac{1}{f/\theta_M + (1 - f)/\theta_G}. \tag{19}$$

The relationship between the TER and C used in metabolism versus growth is shown in figure 2. The maximum value of the TER occurs when C and N are used solely for metabolism, that is, at θ_M, with zero growth. The TER declines as
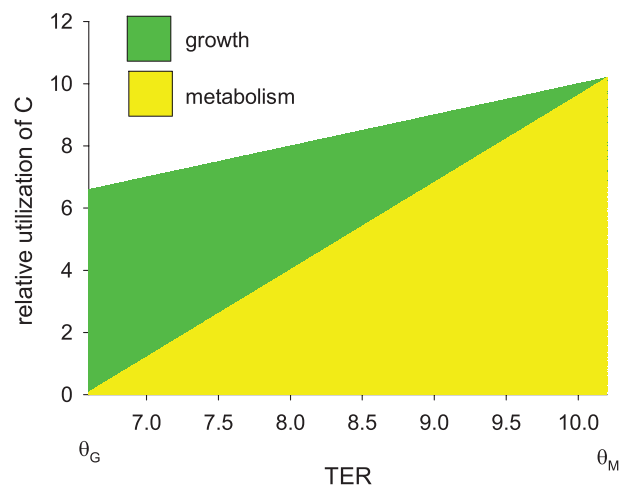

Figure 2: Relative utilization of carbon (C) for growth and metabolism, demonstrating the limits of the threshold elemental ratio (TER; minimum $= \theta_G = 6.6$; maximum $= 10.2$).

the requirements of metabolism become relatively less, with a theoretical minimum equal to θ_G where metabolism is zero. Any food C:N ratio that is external to these bounds (θ_M and θ_G) will automatically lead to a nutritional imbalance for consumers.

Model Validation

The model was first compared to the data of Kiørboe (1989), which are for the marine copepod *Acartia tonsa* grazing the diatom *Thalassiosira weissflogii* cultured to give a range of C:N ratios. This same data set has been used in several previous stoichiometric modeling studies for the purpose of validating the relationship between consumer growth efficiency and food quality (Anderson and Hessen 1995; Kuijper et al. 2004; Acheampong et al. 2014) and was selected for the model-data intercomparison presented here for two reasons. First, new and improved data sets of this kind have not been forthcoming despite more than 25 years having elapsed since Kiør-

boe's measurements. Second, using the Kiørboe (1989) data permits us to directly compare with Anderson and Hessen (1995) and demonstrate the superiority of our current model.

Model predictions for carbon gross growth efficiency (GGE; growth/intake) as a function of food quality, with parameters as in table 2, are compared with corresponding data (Kiørboe 1989) in figure 3a. Excellent agreement is seen between model and data, with a predicted TER of 7.12 mol C mol N^{-1} (fig. 3a). Carbon limits growth when food C:N is less than the TER, with GGE equal to $\beta_C \kappa_C^*$. Predicted growth efficiency declines for food C:N > TER as limitation by N becomes progressively more severe, with respiration increasing markedly as excess C is released as CO_2 in order to maintain homeostasis (fig. 3c).

The data for nitrogen GGE appear to show a more or less constant relationship with increasing food C:N at ~0.4 (fig. 3b). In marked contrast, the model shows a maximum GGE for N of 0.53 at the TER, with GGE declining for lower C:N because dietary N is in stoichiometric excess, as well as for
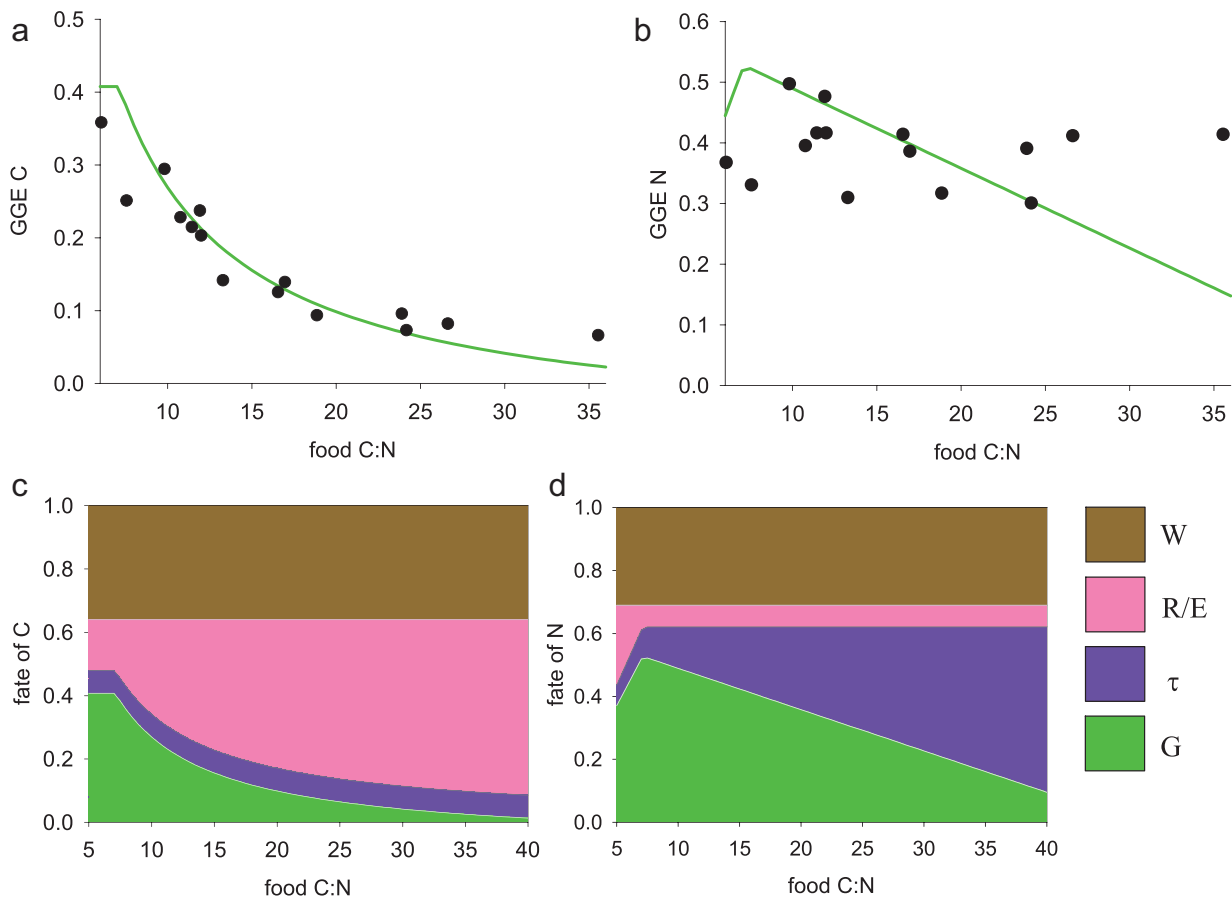

Figure 3: Model predictions for gross growth efficiency (GGE) for carbon (C; *a*) and GGE for nitrogen (N; *b*), with food C:N between 6 and 36. Data are from the experiments of Kiørboe (1989), which were carried out at 17°C. Predicted fate of C (*c*) and N (*d*): growth (G; green), biomass turnover (τ; purple), respiration/excretion excluding τ (R/E; pink), and fecal pellets (W; brown). Intake $I_C = 1.3$ mol C mol C^{-1} day^{-1}, with no temperature dependence and parameters otherwise as in table 2.

higher food C:N as the costs of N in metabolism (parameter τ) become a proportionally greater fraction of intake (fig. 3b, 3d). This pattern leads to a visibly obvious mismatch with the data for food C:N > 25, as the predicted GGE for N continues to decline toward zero. There are two reasons why the model should not be dismissed as unsatisfactory, despite this mismatch with data. First, it is hard to provide a theoretical explanation as to how constant GGE, as shown by the data, could be conserved with increasing food C:N because animals become starved of N and growth (taken to include egg production) declines, as does the GGE for N (fig. 3d). Nitrogen starvation could be partially offset by increasing absorption efficiency for N under nutrient-deplete conditions (Darchambeau et al. 2005; Mitra and Flynn 2005), although not to the extent that high and constant GGE could be maintained. Second, we suggest that the model data mismatch is due to methodological errors associated with the estimation of GGE N based on egg production (as undertaken by Kiørboe 1989) for copepods exposed to food severely depleted in N (high C:N). Animals exploit maternal biomass as an alternate source of N for egg production in this situation, for example, as shown for the copepod *Calanus finmarchicus* (Mayor et al. 2009). There is no new growth as such—that is, no conversion of food to biomass—and so GGE (calculated from egg production/intake) is overestimated (Hirst and McKinnon 2001).

It should be noted that model predictions for GGE N presented herein are a major improvement on those of Anderson and Hessen (1995), which grossly overestimated GGE because their model did not include the costs of N in maintenance. Note also that the model parameter values were all selected from the literature. We investigated parameter tuning as a possible means of improving the fit shown in figure 3b but were unable to achieve much improvement because the biphasic relationship between GGE N and food C:N, with inflection at the TER, is a fundamental property generated by the model. We therefore chose to adhere to our literature-justified parameter values, noting that marginal alterations in the degree of misfit between model and data have no bearing on our findings or conclusions.

The second part of the validation exercise demonstrates the ability of the model to reproduce the observed trends of increasing intake (Durbin and Durbin 1992; Almeda et al. 2010; Yang et al. 2016) and growth (Gresens 1997; Campbell et al. 2001; Sogard and Olla 2001; Kendrick and Bernard 2013; Hayes et al. 2015; Yang et al. 2016) with increasing temperature, using a Q_{10} for intake (parameter I_{max}) of 2. Model results were compared with experimental data for the benthic ciliate *Condylostoma spatiosum* feeding on the dinoflagellate *Oxyrrhis marina* (Li et al. 2011; fig. 4). Multidimensional data sets of this kind are scarce, and we are unaware of any corresponding data for metazoans. These particular data were chosen because they provide simultaneous information on inges-

tion and growth as influenced by both food availability and temperature. Despite the fact that no attempt was made to reparameterize the model for this new scenario, excellent qualitative agreement was seen between model predictions and the data. Growth was observed to increase with increasing temperature in both the data and model predictions (fig. 4). This increase in predicted growth is enabled by the extra intake associated with elevated temperature, which more than compensates for the additional losses in metabolism.

A point of interest regarding the above analysis is to examine the sensitivity of predicted growth rate to the Q_{10} for intake (parameter Q_{IC}) maintaining a fixed value for the Q_{10} for metabolism of 2.0 (fig. 5). Results show that the predicted Q_{10} scaling for growth is equal to 2 when both metabolism and intake also have a Q_{10} of 2, with all three processes responding to temperature in tandem. Metabolism dominates over intake when $Q_{IC} < 2$, leading to a diminished response of growth to increasing temperature. Indeed, the net effects of temperature and metabolism exactly cancel each other, giving zero net change in predicted growth (for a 10°C increase in temperature), when $Q_{IC} = 1.56$ for $I_C = 0.5$ day^{-1} and when $Q_{IC} = 1.28$ for $I_C = 1.0$ day^{-1}. Our choice of $Q_{IC} = 2.0$ is justified on the basis of observed estimates of the temperature response of intake (Kiørboe et al. 1982; Durbin and Durbin 1992; Julian et al. 2001; Almeda et al. 2010), as well as the fact that the growth of invertebrates is often seen to have a Q_{10} of between 2 and 3 (Gresens 1997; Li et al. 2011; Yang et al. 2016).

Testing the Hypothesis: Temperature, Metabolism, and Food C:N Requirement

The validation exercises presented above showed that it is important to consider the effect of temperature on both metabolism and intake when studying how the nutrition of consumers will respond to warming climate. The effect of metabolism is analyzed in this section, with no influence of temperature on intake, and then the combined effect of temperature on metabolism and intake is examined in the next section.

Given that metabolism has a high C:N ratio relative to growth ($\theta_M = 10.2$; $\theta_G = 6.6$), it is straightforward to hypothesize that increasing metabolic costs associated with elevated temperature will mean that invertebrate consumers require increasingly C-rich (high C:N) food in a warming world. TER increases at elevated temperature, while C GGE declines, due to the increasing costs of C in metabolism (fig. 6). These effects are greatest at low intake because metabolism then dominates the overall C budget. Results thus indicate that the C:N of optimal diet, which is equal to the TER, does indeed increase with increasing temperature. This increase is, however, generally rather small except at low
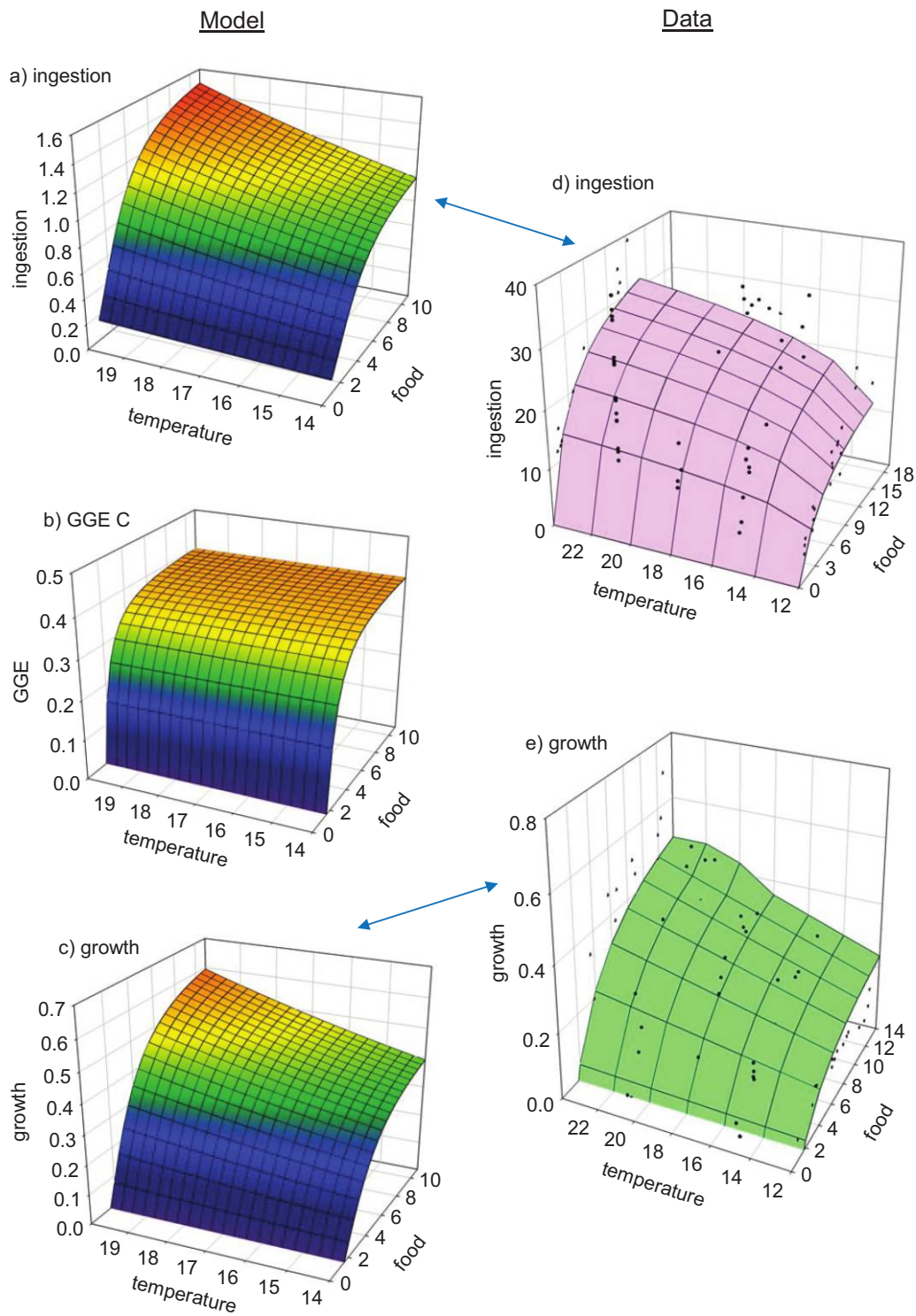
Figure 4: Model predictions as a function of temperature and food availability: ingestion (*a*), gross growth efficiency (GGE) of carbon (C; *b*), and growth (*c*). Predictions for ingestion and growth are compared with experimental results for the benthic ciliate *Condylostoma spatiosum* feeding on a heterotrophic dinoflagellate (*d* and *e* are redrawn from Li et al. 2011, © Inter-Research, used with permission).
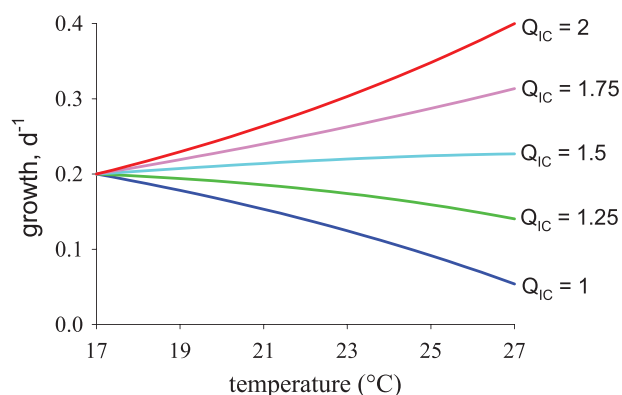
Figure 5: Model sensitivity analysis for the influence of the temperature quotient (Q_{10}) of intake (parameter Q_{IC}) on predicted growth as affected by temperature. Growth rate is 0.2 day^{-1} at 17°C ($I_C = 0.67$ day^{-1}, $\theta_f = 7.73$ = threshold elemental ratio).

intake; for example, it increases from 7.5 at 17°C to 8.0 at 22°C, for an intake of 0.8 day^{-1}.

In reality, animals are commonly exposed to nonoptimal diets in terms of C∶N ratio, with one element limiting growth and the other in stoichiometric excess. How will dietary C∶N imbalance influence the C∶N requirements of invertebrates in a warming world? In order to answer this question, consider three consumers: (*a*) one eating an optimal diet (food C∶N, θ_f = TER), (*b*) one eating a low C∶N diet ($\theta_f <$ TER leading to C limitation of growth), and (*c*) one eating a high C∶N diet ($\theta_f >$ TER, with growth limited by N). Each consumes a ration (I_C) that gives rise to a growth rate, *G*, of 0.2 day^{-1}, for a reference temperature of 17°C. If the three consumers each experience an increase in temperature to 22°C, and they continue eating the same diet (both quality and

quantity), the resulting growth and metabolism, illustrating the stoichiometric fate of C and N, is shown in figure 7.

Consumer *a* has an optimal diet at 17°C ($\theta_f = 7.73$ = TER), meaning that the C and N requirements for growth and metabolism are catered for exactly, with neither element in stoichiometric excess. The costs of metabolism increase when temperature is elevated to 22°C, and so predicted growth decreases from 0.2 to 0.14 day^{-1}. The relative requirement for C increases by more than that for N at the higher temperature (TER increases) because of the high C∶N of metabolism ($\theta_M = 10.2$). Thus, if consumer *a* continues eating the same diet ($\theta_f = 7.73$), C becomes limiting for growth and a small excess of dietary N occurs. This consumer should therefore favor a higher C∶N diet at the elevated temperature, in support of the hypothesis.

Consumer *b*, meanwhile, has access to food with a C∶N ratio of 5.0, which, being less than the TER of 7.73, means that growth is limited by C. The C ration required to achieve $G = 0.2$ day^{-1} is the same as that of consumer *a*, namely, $I_C = 0.67$ day^{-1} at 17°C. Dietary N is, however, in excess. The extra C and N required for metabolism at the higher temperature are equivalent to those experienced by consumer *a*, and predicted growth rate is likewise 0.14 day^{-1}. The stoichiometric excess of N is exacerbated at 22°C, and consumer *b* should continue to prefer a high C∶N diet, again supporting the hypothesis.

In contrast to the first two consumers, consumer *c* experiences a high C∶N diet of 12 ($\theta_f >$ TER), leading to limitation of growth by N. It has to consume a greater ration ($I_C = 1.03$ day^{-1}) in order to provide enough N to achieve $G = 0.2$ day^{-1} at 17°C, and so C is in stoichiometric excess. As with the first two consumers, metabolism increases at 22°C. The resulting decrease in growth is, however, less, $G = 0.16$ day^{-1}, because consumer *c* continues to be limited by N at
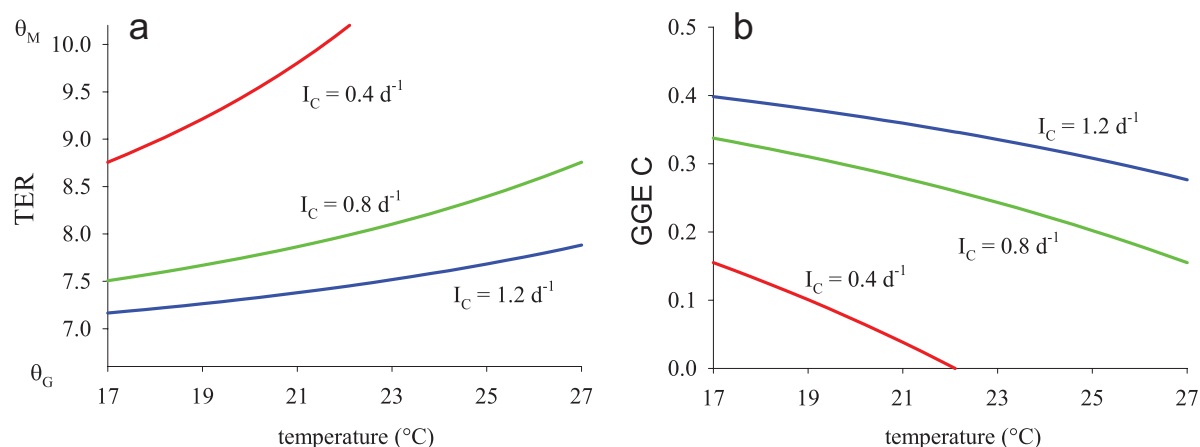

Figure 6: Effect of temperature on threshold elemental ratio (TER; *a*) and carbon gross growth efficiency (GGE; *b*) for three intake rates, $I_C = 0.4$, 0.8, and 1.2 day^{-1}.
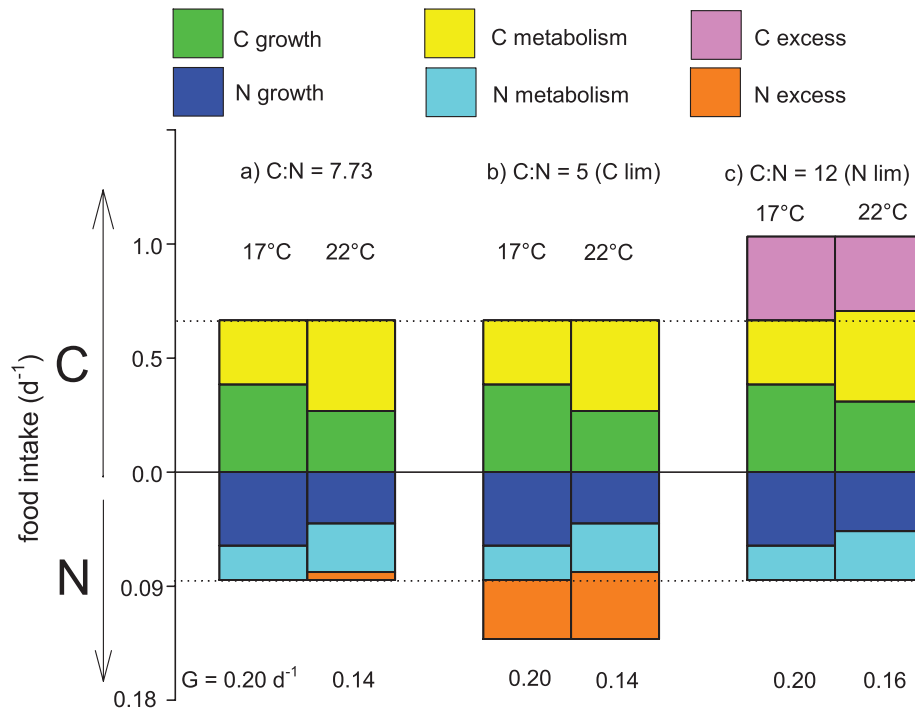
Figure 7: Comparison of utilization of food by three consumers ingesting food of different carbon to nitrogen (C:N) ratios (7.73 = threshold elemental ratio at 17°C; 5 = C limited; 12 = N limited) and at two temperatures (17°C, 22°C). Intake (I_C) is set to achieve a growth rate of 0.2 day^{-1} at 17°C and kept at the same level at 22°C. Excess C and N due to stoichiometric imbalance are shown. The N scale has been extended in proportion to the zooplankton C:N ratio, 5.5, to facilitate the comparison. Growth rates are presented below the bars.

the higher temperature and the increasing costs of metabolism are lower for N relative to C. Most significantly, consumer *c* can meet the increasing costs of C in metabolism at the higher temperature from the stoichiometric excess of this element. It remains limited by N, and therefore, counter to the hypothesis, should not favor C-rich diets with warming; rather, it will continue to prefer N-rich food. Note, however, that there is a special case, namely, that of an animal that is marginally N limited; that is, consuming a diet is only slightly suboptimal in terms of food quality, which switches to limitation by C at elevated temperature because of the increasing costs of C relative to N in metabolism. The model indicates that this scenario will occur only when food C:N ratio is close to the TER because the relative demand for C increases only slowly with increasing temperature. In the case of consumer *a*, for example, the TER increases from 7.73 at 17°C to 8.34 at 22°C for an intake, I_C, of 0.67 day^{-1}.

Testing the Hypothesis: Taking Account of Food Quantity (Intake)

We now repeat the analysis of the last section, but including the effects of temperature on both metabolism and intake (using a Q_{10} of 2 in each case). The predicted effects of tem-

perature on TER and C GGE are shown in figure 8 for $Q_{IC} = 1$ (no effect of temperature on intake) and $Q_{IC} = 1.5, 2$ (e.g., compare the results with those of fig. 6). Remarkably, both TER and GGE are constant, independent of temperature, when metabolism and intake scale equally with temperature (in this case, each has a Q_{10} of 2). In other words, intake and metabolism increase with temperature in tandem and, at least for optimal diet (equal to the TER), the relative demand for C versus N remains unchanged. This result can be deduced directly from the equation for the TER (eq. [6]): providing ζ/I_C remains constant—that is, other basal metabolism (parameter ζ) and intake scale equally with temperature—the TER is also constant.

Finally, we revisit the case of consumers experiencing stoichiometrically imbalanced diets (fig. 9). Consider once again the case of consumer *a*, operating at an optimal food C:N ratio that is equal to the TER ($\theta_f = 7.73$). Elevated temperature increases the cost of metabolism at 22°C, but this is compensated for by the extra intake (which increases from 0.67 day^{-1} to 0.94 day^{-1}). The TER remains unchanged, and the relative allocation of C and N between growth and intake remains the same at the higher temperature, with no stoichiometric excess of either element. GGE is likewise maintained and so, with the extra intake, predicted growth increases
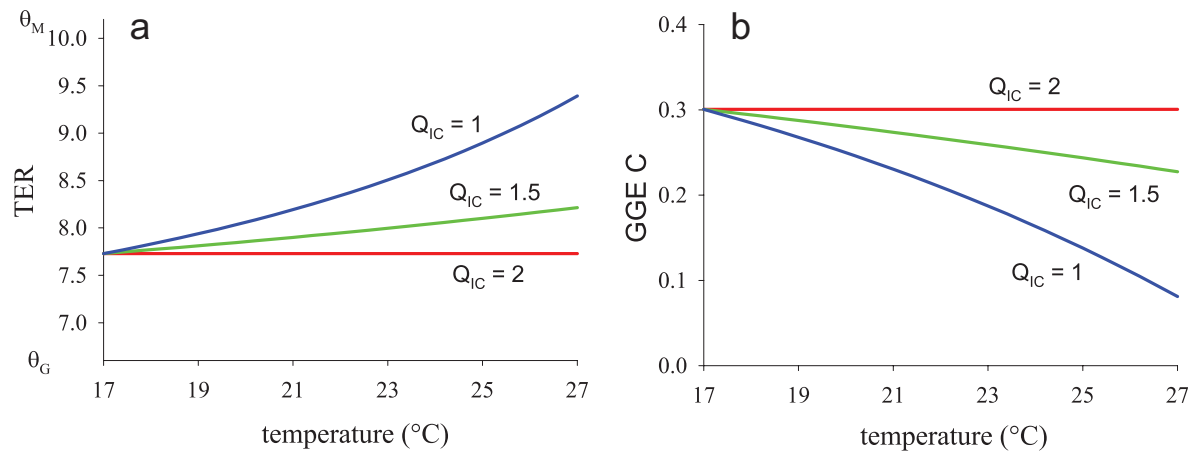
Figure 8: Effect of temperature on threshold elemental ratio (TER; *a*) and carbon gross growth efficiency (GGE; *b*) for $Q_{IC} = 1$ (no effect of temperature on intake), $Q_{IC} = 1.5$, and $Q_{IC} = 2$.

from 0.2 at 17°C to 0.28 at 22°C. Moving on to consumers *b* and *c*, the relative allocations of C and N between growth, metabolism, and stoichiometric excess are also maintained at the higher temperature, as for consumer *a*. In the case of consumer *c*, for example, C is divided 37%, 27%, and 36% between growth, metabolism, and excess C, respectively, and N

is divided 68% and 32% between growth and metabolism, respectively, with no difference between 17°C and 22°C. Growth increases from 0.2 to 0.28 day^{-1} in each case. In other words, the relative dietary requirements for C and N remain unchanged at the higher temperature. Consumer *a* should prefer to keep the same diet because the TER remains unchanged
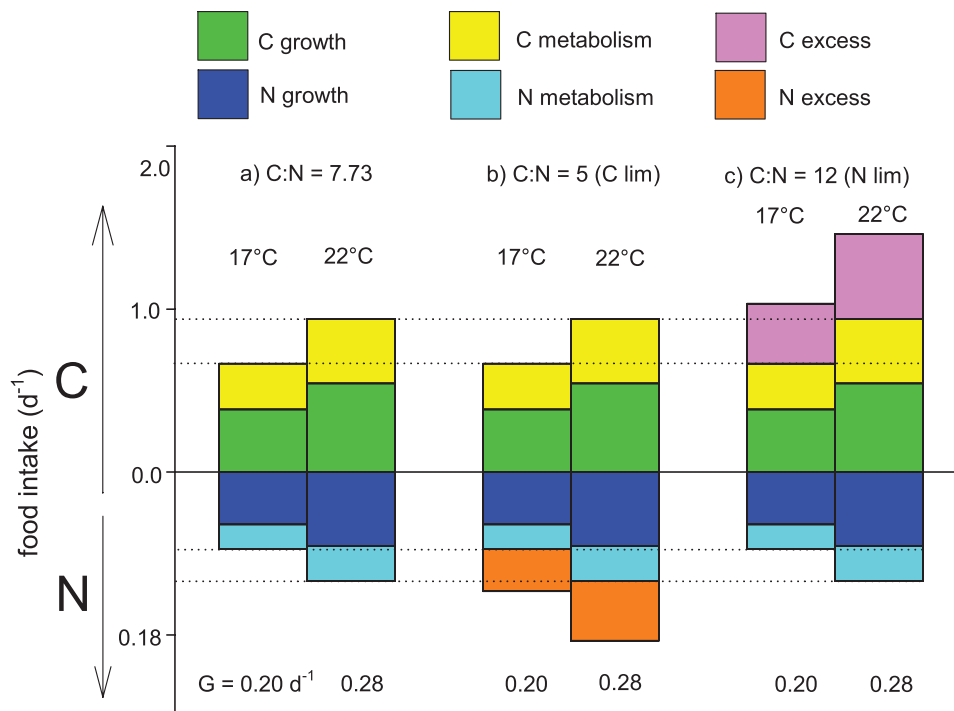

Figure 9: Comparison of utilization of food by three consumers ingesting food of different carbon to nitrogen (C:N) ratios (7.73 = threshold elemental ratio at 17°C; 5 = C limited; 12 = N limited) and at two temperatures (17°C, 22°C). Intake (I_C) is set to achieve a growth rate of 0.2 day^{-1} at 17°C and increases with temperature ($Q_{IC} = 2$) at 22°C. Layout is as for figure 7.

between 17°C and 22°C. Consumer *b* is C limited and so should prefer a C-rich (energy-rich) diet, although not necessarily increasingly so at the higher temperature. Consumer *c* remains limited by N and should continue to prefer N-rich diets, contrary to the hypothesis that consumers will require increasingly C-rich diets at elevated temperature. Dietary stoichiometric imbalance is thereby preserved from one temperature to another.

Discussion

We examined the consequences of increasing temperature for invertebrate nutrition using a new stoichiometric model that has C and N as currencies, includes costs associated with each element in metabolism, treats the synthesis of new and replacement biomass (i.e., replacing that lost in turnover) as one and the same biochemical process, and that applies temperature dependence to metabolism and intake. Specifically, we tested the hypothesis that invertebrate consumers will require increasingly C-rich diets in a warming environment. The hypothesis was shown to be supported for the simplistic case in which an animal consuming an optimal diet (expressed as C∶N ratio, optimal being equal to the TER, meaning that neither C nor N is in excess) and where temperature affects metabolism but not intake. This consumer experiences an increasing requirement for C relative to N with increasing temperature due to the C-rich costs of metabolism and should therefore favor increasingly C-rich diets. This scenario is, however, unrealistic for two reasons, namely, that consumer diet is often nonoptimal in the first place and that temperature affects not only metabolism but intake also. When these factors are taken into consideration, the results of our modeling study indicate an entirely different conclusion: the nutritional requirements of invertebrate consumers may change little, if at all, at elevated temperature. The intuitively appealing hypothesis that consumers should require food increasingly rich in C (energy) in a warming world is thereby unsupported.

The growth of invertebrates, including zooplankton and insects, may commonly be limited by nutrient elements (Hessen 1992; DeMott et al. 2001; Frost and Elser 2002; Huberty and Denno 2006), and animals are often observed to select for nutrient-rich diets (Mattson 1980; Cowles et al. 1988; Minkenberg and Ottenheim 1990; White 1993; Meunier et al. 2016). The resulting excess of C has important physiological, ecological, and evolutionary consequences for animal fitness (Hessen and Anderson 2008) and broader implications for the biogeochemistry of ecosystems (Hessen et al. 2004; Anderson et al. 2013). With regard to the hypothesis, our model demonstrates that an N-limited consumer will not experience an increasing demand for dietary C with increasing temperature because the increased costs of C in metabolism can be met from the stoichiometric excess. This intuitive result

has been overlooked in previous stoichiometric studies examining the effect of temperature on consumer nutrition. Animals limited by N will therefore remain limited and should continue to prefer N-rich diets at elevated temperatures, all the more so because metabolism involves not only C but nutrient elements as well. Indeed, the demand for N increases with increasing temperature, for example, due to losses of N in protein turnover (Hachiya et al. 2007; Mayor et al. 2011; Ikeda 2014). There is one special case regarding this prediction, namely, that an N-limited animal could switch to being limited by C at elevated temperature. In fact, however, our analysis indicates that this would occur only if the animal was feeding on a diet close to the optimum food C∶N ratio because the TER increases rather slowly with increasing temperature; for example, it increases from 7.5 at 17°C to 8.0 at 22°C, for an intake of 0.8 day^{-1} (fig. 6).

The analysis described above assumes that intake is fixed and unaffected by temperature, in which case, predicted growth efficiency and growth itself decrease with increasing temperature because of the increasing costs of metabolism. Growth is, however, inextricably linked to metabolism (West et al. 2001; Zuo et al. 2010) and should therefore increase with temperature, providing sufficient food is consumed to provide the necessary substrates. The results of observation and experiment do indeed show that growth rate increases with increasing temperature in a range of consumers including insects, zooplankton, and fish (Gresens 1997; Campbell et al. 2001; Sogard and Olla 2001; Kendrick and Bernard 2013; Hayes et al. 2015; Yang et al. 2016) and that poikilothermic invertebrates increase food intake when exposed to elevated temperatures (Durbin and Durbin 1992; Almeda et al. 2010; Li et al. 2011; Yang et al. 2016), providing a means to offset the increased demands of metabolism (O'Connor et al. 2011). Foraging and feeding activities increase at elevated temperature in a wide range of animals (Greenwald 1974; Gill and Crisp 1985; Van Damme et al. 1991; Herrel and Bonneaud 2012; Moison et al. 2012) as a consequence of faster-acting skeletomuscular, nervous, and respiratory systems (Marsh and Bennett 1985; Van Damme et al. 1991).

The analysis was therefore extended to examine the simultaneous effects of temperature on metabolism and intake, using a Q_{10} of 2 for each process. The outcome was striking: model predictions showed that there is no net effect of increasing temperature on the relative nutritional requirement for C and N because the increased costs of metabolism are counterbalanced by the increased C and N obtained via intake. If both metabolism and intake are temperature dependent, with the same Q_{10}, then metabolism as a fraction of total intake, and thereby the relative allocations of C and N to metabolism versus growth, and the optimal food C∶N ratio (the TER) all remain unchanged. Furthermore, the same situation holds for animals experiencing stoichiometrically imbalanced diets. The relative allocation of intake between

growth, metabolism, and excess C or N remains unchanged when the effects of temperature on metabolism and intake counterbalance each other, whether or not the diet matches the TER. The extent to which a consumer is limited by C or N therefore remains unaltered with increasing temperature. An N-limited consumer, for example, remains limited by N and will continue to favor N-rich diets in a warming climate. The hypothesis that consumers require increasingly C-rich diets in a warming environment is therefore unsupported.

The Q_{10} for intake (parameter Q_{IC}) need not necessarily match that of metabolism in reality (both were set to 2 in our analysis). Although a few studies have shown a low value for intake relative to the Q_{10} for metabolism (Kingsolver and Woods 1997; Rall et all. 2010; Lemoine and Burkepile 2012), there are equally studies that exhibit Q_{IC} values ≫ 2 (Kiørboe et al. 1982; Hansen et al. 1997 and references therein). Our choice of $Q_{IC} = 2$ is justified not only as a representative average of values seen in the literature (including studies that show Q_{IC} in the region of 2; Kiørboe et al. 1982; Durbin and Durbin 1992; Julian et al. 2001; Almeda et al. 2010), but also because, as our analysis showed, Q_{IC} of at least 2 is needed in order to predict observed Q_{10} scaling for growth of between 2 and 3 (Gresens 1997; Li et al. 2011; Yang et al. 2016).

There are two stoichiometric caveats to our work. First, it should be noted that our analysis deals explicitly with growth rate responses that exclude the sequestration of C-rich energy reserves, for example, lipid storage by zooplankton (Lee et al. 2006; Aubert et al. 2013), which are required to sustain widely adopted invertebrate life-history strategies such as diapause. Second, many consumers, particularly those in freshwater systems, are limited by phosphorus (P) rather than N (Sterner and Elser 2002). The biochemical pathways and cycling of N and P by organisms are somewhat different; for example, N is associated primarily with protein synthesis, while P is involved in nucleic acids and energy transfer via ATP (Elser 2006). Our conclusions pertaining to nutrient limitation based on N, as affected by temperature, should therefore only be generalized to include other nutrient elements, notably P, with due care.

Our work has highlighted the complex nature of the effect of temperature on organisms, emphasizing the need for further experimental studies and improved data sets that simultaneously address food quality, quantity, and the effects of temperature on metabolism and intake. Better physiological understanding is needed of how temperature affects metabolism and growth, as well as intake, in organisms. Metabolism, for example, comprises the turnover of a range of macromolecules including proteins, lipids, and so on, each of which may be impacted differently by temperature. The use of Q_{10} as a scaling metric also merits attention. Many animals are adapted to survive within a thermal window (Pörtner and Farrell 2008; Mayor et al. 2015), exhibiting temperature optima at which their enzyme systems operate most efficiently.

The relationship between temperature and growth efficiency or growth is then parabolic (Iguchi and Ikeda 1995; McCarthy et al. 1998; Heilmayer et al. 2004; Handeland et al. 2008; Niehaus et al. 2012). Likewise, the maximum rate of ingestion may also be subject to a temperature optimum (Garrido et al. 2013). A further consideration is that animals experience variations in temperature on a range of spatiotemporal scales, often quite short (Pincebourde and Woods 2012). Vertically migrating zooplankton, for example, may experience large fluctuations in temperature and food quality over short time intervals (Sterner and Schwalbach 2001). Integrating physiology and associated stoichiometry in such instances poses a significant challenge and must take into account the ability of organisms to acclimate to warming or how they may adapt in the face of long-term change to environmental temperatures and the quantity and quality of their food.

Elevated C∶N ratios are seen in both plant leaves and algae as a consequence of changing climate, due to both increased warming (An et al. 2005; Sardans et al. 2008; Makino et al. 2011; Sardans and Peñuelas 2013) and elevated CO_2 levels (Gifford et al. 2000; Urabe and Waki 2009; Sardans et al. 2012). Increasing stratification of the ocean also promotes a greater C∶N ratio in phytoplankton (Díez et al. 2013; Clarke et al. 2014; Eberlein et al. 2016) via a diminished supply of nutrients to surface waters (Bopp et al. 2001; Steinacher et al. 2010). Our analysis demonstrates that, although the metabolic demand for C increases at elevated temperature, this will not necessarily translate into an increase in the dietary requirement for this element relative to N. Higher C∶N ratios in autotroph biomass are, therefore, unlikely to be of benefit for invertebrate consumers. Indeed, in the case of consumers limited by N, higher ratios will exacerbate the stoichiometric mismatch of plant-herbivore interactions, with important consequences for food web dynamics and the cycling and storage of C and N in ecosystems (Hessen et al. 2004; Anderson et al. 2013).

Acknowledgments

Literature Cited

Acheampong, E., I. Hense, and M. A. St. John. 2014. A model for the description of feeding regulation by mesozooplankton under different conditions of temperature and prey nutritional status. Ecological Modelling 272:84–97.

Acheampong, E., M. H. Nielsen, A. Mitra, and M. A. St. John. 2012. Towards an adaptive model for simulating growth of marine mesozooplankton: a macromolecular perspective. Ecological Modelling 225:1–18.

Almeda, R., C. B. Augustin, M. Alcaraz, A. Calbet, and E. Saiz. 2010. Feeding rates and gross growth efficiencies of larval developmental stages of *Oithona davisae* (Copepoda, Cyclopoida). Journal of Experimental Marine Biology and Ecology 387:24–35.

An, Y., S. Wan, X. Zhou, A. A. Subedar, L. L. Wallace, and Y. Luo. 2005. Plant nitrogen concentration, use efficiency, and contents in a tallgrass prairie ecosystem under experimental warming. Global Change Biology 11:1733–1744.

Andersen, T., and D. O. Hessen. 1991. Carbon, nitrogen and phosphorus content in common crustacean zooplankton species. Limnology and Oceanography 36:807–814.

Anderson, T. R. 1994. Relating C:N ratios in zooplankton food and faecal pellets using a biochemical model. Journal of Experimental Marine Biology and Ecology 184:183–199.

Anderson, T. R., W. C. Gentleman, and B. Sinha. 2010. Influence of grazing formulations on the emergent properties of a complex ecosystem model in a global ocean general circulation model. Progress in Oceanography 87:201–213.

Anderson, T. R., and D. O. Hessen. 1995. Carbon or nitrogen limitation of marine copepods? Journal of Plankton Research 17:317–331.

———. 2005. Threshold elemental ratios for carbon versus phosphorus limitation in *Daphnia*. Freshwater Biology 50:2063–2075.

Anderson, T. R., D. O. Hessen, J. J. Elser, and J. Urabe. 2005. Metabolic stoichiometry and the fate of excess carbon and nutrients in consumers. American Naturalist 165:1–15.

Anderson, T. R., D. O. Hessen, A. Mitra, D. J. Mayor, and A. Yool. 2013. Sensitivity of secondary production and export flux to choice of trophic transfer formulation in marine ecosystem models. Journal of Marine Systems 125:41–53.

Angilletta, M. J., T. D. Steury, and M. W. Sears. 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. Integrative and Comparative Biology 44:498–509.

Aubert, A. B., C. Svensen, D. O. Hessen, and T. Tamelander. 2013. CNP stoichiometry of a lipid-synthesising zooplankton, *Calanus finmarchicus*, from winter to spring bloom in a sub-Arctic sound. Journal of Marine Systems 111–112:19–28.

Barton, B. T., and J. Schmitz. 2009. Experimental warming transforms multiple predator effects in a grassland food web. Ecology Letters 12:1317–1325.

Boersma, M., K. A. Mathew, B. Niehoff, K. L. Schoo, R. M. Franco-Santos, and C. L. Meunier. 2016. Temperature driven changes in the diet preference of omnivorous copepods: no more meat when it's hot? Ecology Letters 19:45–53.

Bopp, L., P. Monfray, O. Aumont, J. Dufresne, H. Le Treut, G. Madec, L. Terray, and J. Orr. 2001. Potential impact of climate change on marine export production. Global Biogeochemical Cycles 15:81–100.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Campbell, R. G., M. M. Wagner, G. J. Teegarden, C. A. Boudreau, and E. G. Durbin. 2001. Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. Marine Ecology Progress Series 221:161–183.

Clarke, D. R., K. J. Flynn, and H. Fabian. 2014. Variation in elemental stoichiometry of the marine diatom *Thalassiosira weissflogii* (Bacillariophyceae) in response to combined nutrient stress and changes in carbonate chemistry. Journal of Phycology 50:640–651.

Cowles, T. J., R. J. Olson, and S. W. Chisholm. 1988. Food selection by copepods: discrimination on the basis of food quality. Marine Biology 100:41–49.

Cross, W. F., J. M. Hood, J. P. Benstead, A. D. Huryn, and D. Nelson. 2015. Interactions between temperature and nutrients across levels of ecological organization. Global Change Biology 21:1025–1040.

Darchambeau, F., I. Thys, B. Leporcq, L. Hoffmann, and J.-P. Descy. 2005. Influence of zooplankton stoichiometry on nutrient sedimentation in a lake system. Limnology and Oceanography 50:905–913.

Deason, E. E. 1981. Grazing of *Acartia hudsonica* (*A. clausi*) on *Skeletonema costatum* in Narragansett Bay (USA): influence of food concentration and temperature. Marine Biology 60:101–113.

Dell, A. I., S. Pawar, and V. M. Savage. 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. Journal of Animal Ecology 83:70–84.

DeMott, W. R., R. D. Gulati, and K. Siewertsen. 1998. Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *Daphnia magna*. Limnology and Oceanography 43:1147–1161.

DeMott, W. R., R. D. Gulati, and E. Van Donk. 2001. Effects of dietary phosphorus deficiency on the abundance, phosphorus balance, and growth of *Daphnia cucullata* in three hypereutrophic Dutch lakes. Limnology and Oceanography 46:1871–1880.

Díez, B., L. van Nieuwerburgh, and P. Snoeijs. 2013. Water nutrient stoichiometry modifies the nutritional quality of phytoplankton and somatic growth of crustacean mesozooplankton. Marine Ecology Progress Series 489:93–105.

Doi, H. M., M. Cherif, T. Iwabuchi, I. Katano, J. C. Stegen, and M. Striebel. 2010. Integrating elements and energy through the metabolic dependencies of gross growth efficiency and the threshold elemental ratio. Oikos 119:752–765.

Durbin, E. G., and A. G. Durbin. 1992. Effects of temperature and food abundance on grazing and short-term weight change in the marine copepod *Acartia hudsonica*. Limnology and Oceanography 37:361–378.

Eberlein, T., D. B. van der Waal, K. M. Brandenburg, U. John, M. Voss, E. P. Achterberg, and B. Rost. 2016. Interactive effects of ocean acidification and nitrogen limitation on two bloom-forming dinoflagellate species. Marine Ecology Progress Series 543:127–140.

Ehnes, R. B., B. C. Rall, and U. Brose. 2011. Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates. Ecology Letters 14:993–1000.

Elendt, B.-P. 1989. Effects of starvation on growth, reproduction, survival and biochemical composition of *Daphnia magna*. Archiv für Hydrobiologie 116:415–433.

Elser, J. 2006. Biological stoichiometry: a chemical bridge between ecosystem ecology and evolutionary biology. American Naturalist 168 (suppl.):S25–S35.

Freitas, V., J. F. M. F. Cardoso, K. Lika, M. A. Peck, J. Campos, S. A. L. M. Kooijman, and H. W. van der Veer. 2010. Temperature tolerance and energetics: a dynamic energy budget-based comparison of North Atlantic marine species. Philosophical Transactions of the Royal Society B 365:3553–3565.

Friberg, N., J. B. Dybkjær, J. S. Olafsson, G. M. Gislason, S. E. Larsen, and T. L. Lauridsen. 2009. Relationships between structure and function in streams contrasting in temperature. Freshwater Biology 54:2051–2068.

Frost, P. C., and J. J. Elser. 2002. Growth responses of littoral mayflies to the phosphorus content of their food. Ecology Letters 5:232–240.

Garrido, S., T. Cruz, A. M. P. Santos, P. Ré, and E. Saiz. 2013. Effects of temperature, food type and food concentration on the grazing of the calanoid copepod *Centropages chierchiae*. Journal of Plankton Research 35:843–854.

Gifford, R. M., D. J. Barrett, and J. L. Lutze. 2000. The effects of elevated [CO_2] on the C : N and C : P mass ratios of plant tissues. Plant and Soil 224:1–14.

Gill, C. W., and D. J. Crisp. 1985. The effect of size and temperature on the frequency of limb beat of *Temora longicornis* Müller (Crustacea: Copepoda). Journal of Experimental Marine Biology and Ecology 86: 185–196.

Gillooly, J. F., J. H. Brown, G. B. West, V. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science 293: 2248–2251.

Gismervik, I. 1997. Stoichiometry of some marine planktonic crustaceans. Journal of Plankton Research 19:279–285.

Greenwald, O. E. 1974. Thermal dependence of striking and prey capture by gopher snakes. Copeia 1974:141–148.

Gresens, S. E. 1997. Interactive effects of diet and thermal regime on growth of the midge *Pseudochironomus richardsoni* Malloch. Freshwater Biology 38:365–373.

Hachiya, T., I. Terashima, and K. Noguchi. 2007. Increase in respiratory cost at high growth temperature is attributed to high protein turnover cost in *Petunia* × *hybrida* petals. Plant, Cell and Environment 30: 1269–1283.

Handeland, S. O., A. K. Imsland, and S. O. Stefansson. 2008. The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon postsmolts. Aquaculture 283:36–42.

Hansen, P. J., P. K. Bjørnsen, and B. W. Hansen. 1997. Zooplankton grazing and growth: scaling within the 2–2,000-μm body size range. Limnology and Oceanography 42:687–704.

Hayes, M. B., L. Jiao, T.-H. Tsao, I. King, M. Jennings, and C. Hou. 2015. High temperature slows down growth in tobacco hornworms (*Manduca sexta* larvae) under food restriction. Insect Science 22: 424–430.

Heilmayer, O., T. Brey, and H. O. Pörtner. 2004. Growth efficiency and temperature in scallops: a comparative analysis of species adapted to different temperatures. Functional Ecology 18:641–647.

Herrel, A., and C. Bonneaud. 2012. Temperature dependence of locomotor performance in the tropical clawed frog, *Xenopus tropicalis*. Journal of Experimental Biology 215:2465–2470.

Hessen, D. O. 1992. Nutrient element limitation of zooplankton production. American Naturalist 140:799–814.

Hessen, D. O., G. I. Ågren, T. R. Anderson, J. J. Elser, and P. De Ruiter. 2004. Carbon sequestration in ecosystems: the role of stoichiometry. Ecology 85:1179–1192.

Hessen, D. O., and T. R. Anderson. 2008. Excess carbon in aquatic organisms and ecosystems: physiological, ecological, and evolutionary implications. Limnology and Oceanography 53:1685–1696.

Hirst, A. G., and A. D. McKinnon. 2001. Does egg production represent adult female copepod growth? a call to account for body weight changes. Marine Ecology Progress Series 223:179–199.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomologist 91:293–320.

Huberty, A. F., and R. F. Denno. 2006. Consequences of nitrogen and phosphorus limitation for the performance of two planthoppers with divergent life-history strategies. Oecologia 149:444–455.

Iguchi, N., and T. Ikeda. 1995. Growth, metabolism and growth efficiency of a euphausiid crustacean *Euphausia pacifica* in the southern Japan Sea, as influenced by temperature. Journal of Plankton Research 17: 1757–1769.

Ikeda, T. 2014. Respiration and ammonia excretion by marine metazooplankton taxa: synthesis toward a global-bathymetric model. Marine Biology 161:2753–2766.

Ikeda, T., Y. Kanno, K. Ozaki, and A. Shinada. 2001. Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. Marine Biology 139:587–596.

IPCC. 2013. Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Irlich, U. M., J. S. Terblanche, T. M. Blackburn, and S. L. Chown. 2009. Insect rate-temperature relationships: environmental variation and the metabolic theory of ecology. American Naturalist 174:819–835.

Julian, D., M. L. Chang, J. R. Rudd, and A. J. Arp. 2001. Influence of environmental factors on burrow irrigation and oxygen consumption in the mudflat invertebrate *Urechis caupo*. Marine Biology 139:163–173.

Karr, J. R., J. C. Sanghvi, D. N. Macklin, M. V. Gutschow, J. M. Jacobs, B. Bolival Jr., N. Assad-Garcia, J. I. Glass, and M. W. Lovert. 2012. A whole-cell computational model predicts phenotype from genotype. Cell 150:389–401.

Kearney, M. R., S. J. Simpson, D. Raubenheimer, and S. A. L. M. Kooijman. 2013. Balancing heat, water and nutrients under environmental change: a thermodynamic niche framework. Functional Ecology 27:950–965.

Kendrick, M. R., and J. P. Benstead. 2013. Temperature and nutrient availability interact to mediate growth and body stoichiometry in a detritivorous stream insect. Freshwater Biology 58:1820–1830.

Kingsolver, J. G., and H. A. Woods. 1997. Thermal sensitivity of growth and feeding in *Manduca sexta* caterpillars. Physiological Zoology 70: 631–638.

Kiørboe, T. 1989. Phytoplankton growth rate and nitrogen content: implications for feeding and fecundity in a herbivorous copepod. Marine Ecology Progress Series 55:229–234.

Kiørboe, T., F. Møhlenberg, and H. Nicolajsen. 1982. Ingestion rate and gut clearance in the planktonic copepod *Centropages hamatus* (Liljeborg) in relation to food concentration and temperature. Ophelia 21: 191–194.

Klaassen, M., and B. A. Nolet. 2008. Stoichiometry of endothermy: shifting the quest from nitrogen to carbon. Ecology Letters 11:785–792.

Kuijper, L. D. J., T. R. Anderson, and S. A. L. M. Kooijman. 2004. C and N gross growth efficiencies of copepod egg production studied using a dynamic energy budget model. Journal of Plankton Research 26: 213–226.

Lee, K. P., T. Jang, N. Ravzanaadii, and M. S. Rho. 2015. Macronutrient balance modulates the temperature-size rule in an ectotherm. American Naturalist 186:212–222.

Lee, K. P., and C. Roh. 2010. Temperature-by-nutrient interactions affecting growth rate in an insect ectotherm. Entomologia Experimentalis et Applicata 136:151–163.

Lee, R. F., W. Hagen, and G. Kattner. 2006. Lipid storage of marine zooplankton. Marine Ecology Progress Series 307:273–306.

Lemcke, H. W., and W. Lampert. 1975. Veränderungen im Gewicht und der chemischen zusammensetzung von *Daphnia pulex* im hunger. Archiv für Hydrobiologie (suppl.) 48:109–137.

Lemoine, N. P., and D. E. Burkepile. 2012. Temperature-induced mismatches between consumption and metabolism reduce consumer fitness. Ecology 93:2483–2489.

Lemoine, N. P., W. A. Drews, D. E. Burkepile, and J. D. Parker. 2013. Increased temperature alters foraging behavior of a generalist herbivore. Oikos 122:1669–1678.

Li, C., K. Xu, and Y. Lei. 2011. Growth and grazing responses to temperature and prey concentration of *Condylostoma spatiosum*, a large benthic ciliate, feeding on *Oxyrrhis marina*. Aquatic Microbial Ecology 64:97–104.

Makino, W., Q. Gong, and J. Urabe. 2011. Stoichiometric effects of warming on herbivore growth: experimental test with plankters. Ecosphere 2(7):art79, http://dx.doi.org/10.1890/ES11-00178.1.

Malzahn, A. M., D. Doerfler, and M. Boersma. 2016. Junk food gets healthier when it's warm. Limnology and Oceanography 61:1677–1685.

Marsh, R. L., and A. F. Bennett. 1985. Thermal dependence of isotonic contractile properties of skeletal muscle and sprint performance of the lizard *Dipsosaurus dovsalis*. Journal of Comparative Physiology B 155:541–551.

Mattson, W. J., Jr. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11:119–161.

Mayor, D. J., T. R. Anderson, D. W. Pond, and X. Irigoien. 2009. Egg production and associated losses of carbon, nitrogen and fatty acids from maternal biomass in *Calanus finmarchicus* before the spring bloom. Journal of Marine Systems 78:505–510.

Mayor, D. J., K. Cook, B. Thornton, P. Walsham, U. F. M. Witte, A. F. Zuur, and T. R. Anderson. 2011. Absorption efficiencies and basal turnover of C, N and fatty acids in a marine Calanoid copepod. Functional Ecology 25:509–518.

Mayor, D. J., U. Sommer, K. B. Cook, and M. R. Viant. 2015. The metabolic response of marine copepods to environmental warming and ocean acidification in the absence of food. Nature Scientific Reports 5:13690, http://dx.doi.org/10.1038/srep13690.

McCarthy, I., E. Moksness, and D. A. Pavlov. 1998. The effects of temperature on growth rate and growth efficiency of juvenile common wolfish. Aquaculture International 6:207–218.

Mente, E., P. Coutteau, D. F. Houlihan, I. Davidson, and P. Sorgeloos. 2002. Protein turnover, amino acid profile and amino acid flux in juvenile shrimp *Litopenaeus vannamei*: effects of dietary protein source. Journal of Experimental Biology 205:3107–3122.

Meunier, C. L., M. Boersma, K. H. Wiltshire, and A. M. Malzahn. 2016. Zooplankton eat what they need: copepod selective feeding and potential consequences for marine systems. Oikos 125:50–58.

Minkenberg, O. P. J. M., and J. J. G. W. Ottenheim. 1990. Effect of leaf nitrogen content of tomato plants on preference and performance of a leafmining fly. Oecologia 83:291–298.

Mitra, A., and K. J. Flynn. 2005. Predator-prey interactions: is "ecological stoichiometry" sufficient when good food goes bad? Journal of Plankton Research 27:393–399.

Moison, M., F. G. Schmitt, and S. Souissi. 2012. Effect of temperature on *Temora longicornis* swimming behaviour: illustration of seasonal effects in a temperate ecosystem. Aquatic Biology 16:149–162.

Niehaus, A. C., M. J. Angilletta, M. W. Sears, C. E. Franklin, and R. S. Wilson. 2012. Predicting the physiological performance of ectotherms in fluctuating thermal environments. Journal of Experimental Biology 215:694–701.

O'Connor, M. I., B. Gilbert, and C. J. Brown. 2011. Theoretical predictions for how temperature affects the dynamics of interacting herbivores and plants. American Naturalist 178:626–638.

Penry, D. 1998. Applications of efficiency measurements in bioaccumulation studies: definitions, clarifications, and a critique of methods. Environmental Toxicology and Chemistry 17:1633–1639.

Persson, J., M. W. Wojewodzic, D. O. Hessen, and T. Andersen. 2011. Increased risk of phosphorus limitation at higher temperatures for *Daphnia magna*. Oecologia 165:123–129.

Pincebourde, S., and H. A. Woods. 2012. Climate uncertainty on leaf surfaces: the biophysics of leaf microclimates and their consequences for leaf-dwelling organisms. Functional Ecology 26:844–853.

Pörtner, H. O., and A. P. Farrell. 2008. Physiology and climate change. Science 322:690–692.

Rall, B., O. Vucic-Pestic, R. B. Ehnes, M. Emmerson, and U. Brose. 2010. Temperature, predator-prey interaction strength and population stability. Global Change Biology 16:2145–2157.

Roman, M. R. 1983. Nitrogenous nutrition of marine invertebrates. Pages 347–383 *in* E. J. Carpenter and D. G. Capone, eds. Nitrogen in the marine environment. Academic Press, New York.

Sardans, J., and J. Peñuelas. 2013. Plant-soil interactions in Mediterranean forest and shrublands: impacts of climatic change. Plant and Soil 365:1–33.

Sardans, J., J. Peñuelas, and R. Ogaya. 2008. Drought-induced changes in C and N stoichiometry in a *Quercus ilex* Mediterranean forest. Forest Science 54:513–522.

Sardans, J., A. Rivas-Ubach, and J. Peñuelas. 2012. The C:N:P stoichiometry of organisms and ecosystems in a changing world: a review and perspectives. Perspectives in Plant Ecology, Evolution and Systematics 14:33–47.

Schmitz, O. J., A. E. Rosenblatt, and M. Smylie. 2016. Temperature dependence of predation stress and the nutritional ecology of a generalist herbivore. Ecology 97:3119–3130, http://dx.doi.org/10.1002/ecy.1524.

Schoo, K. L., A. M. Malzahn, E. Krause, and M. Boersma. 2013. Increased carbon dioxide availability alters phytoplankton stoichiometry and affects carbon cycling and growth of a marine planktonic herbivore. Marine Biology 160:2145–2155.

Secor, S. M. 2009. Specific dynamic action: a review of the postprandial metabolic response. Journal of Comparative Physiology B 179:1–56.

Secor, S. M., J. A. Wooten, and C. L. Cox. 2007. Effects of meal size, meal type, and body temperature on the specific dynamic action of anurans. Journal of Comparative Physiology B 177:165–182.

Sogard, S. M., and B. L. Olla. 2001. Growth and behavioral responses to elevated temperatures by juvenile sablefish *Anoplopoma fimbria* and the interactive role of food availability. Marine Ecology Progress Series 217:121–134.

Steinacher, M., F. Joos, T. L. Frölicher, L. Bopp, P. Cadule, V. Cocco, S. C. Doney, et al. 2010. Projected 21st century decrease in marine productivity: a multi-model analysis. Biogeosciences 7:979–1005.

Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, NJ.

Sterner, R. W., and M. S. Schwalbach. 2001. Diel integration of food quality by *Daphnia*: luxury consumption by a freshwater planktonic herbivore. Limnology and Oceanography 46:410–416.

Teal, L. R., R. van Hal, T. van Kooten, P. Ruardij, and A. D. Rijnsdorp. 2012. Bio-energetics underpins the spatial response of North Sea plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) to climate change. Global Change Biology 18:3291–3305.

Thor, P., G. Cervetto, S. Besiktepe, E. Ribera-Maycas, K. W. Tang, and H. G. Dam. 2002. Influence of two different green algal diets on specific dynamic action and incorporation of carbon into biochemical fractions in the copepod *Acartia tonsa*. Journal of Plankton Research 24:293–300.

Traill, L. W., M. L. Lim, N. S. Sodhi, and C. J. A. Bradshaw. 2010. Mechanisms driving change: altered species interactions and ecosystem function through global warming. Journal of Animal Ecology 79:937–947.

Urabe, J., and N. Waki. 2009. Mitigation of adverse effects of rising CO_2 on a planktonic herbivore by mixed algal diets. Global Change Biology 15:523–531.

Urabe, J., and Y. Watanabe. 1991. Effect of food concentration on the assimilation and production efficiencies of *Daphnia galeata* G.O. Sars (Crustacea: Cladocera). Functional Ecology 5:635–641.

Van Damme, R., D. Bauwens, and R. F. Verheyen. 1991. The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. Functional Ecology 5:507–517.

Vucic-Pestic, O., R. B. Ehnes, B. C. Rall, and U. Brose. 2011. Warming up the system: higher predator feeding rates but lower energetic efficiencies. Global Change Biology 17:1301–1310.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

West, G. B., J. H. Brown, and B. J. Enquist. 2001. A general model for ontogenetic growth. Nature 413:628–631.

White, T. C. R. 1993. The inadequate environment: nitrogen and the abundance of animals. Springer, Berlin.

Yang, Z., L. Zhang, X. Zhu, J. Wang, and D. J. S. Montagnes. 2016. An evidence-based framework for predicting the impact of differing autotroph-heterotroph thermal sensitivities on consumer-prey dynamics. ISME Journal 10:1767–1778.

Zhang, P., B. A. Blonk, R. F. van den Berg, and E. S. Bakker. 2016. The effect of temperature on herbivory by the omnivorous ectotherm snail *Lymnaea stagnalis*. Hydrobiologia, http://dx.doi.org/10.1007/s10750-016-2891-7.

Zhu, K. Y., H. Merzendorfer, W. Zhang, J. Zhang, and S. Muthukrishnan. 2016. Biosynthesis, turnover, and functions of chitin in insects. Annual Review of Entomology 61:177–196.

Zuo, W., M. E. Moses, G. B. West, C. Hou, and J. H. Brown. 2010. A general model for effects of temperature on ectotherm ontogenetic growth and development. Proceedings of the Royal Society B 279:1840–1846.

Calanus finmarchicus, one of the most common animals (copepods) found in the North Atlantic and northern North Sea. These tiny creatures (~2 mm) provide a crucial link in the food chain between microscopic algae and fish. Photo: Daniel J. Mayor.