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Intraspecific temperature dependence of the scaling of metabolic rate with body mass in fishes and its ecological implications

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Metabolism constitutes a fundamental property of all organisms. Metabolic rate is commonly described to scale as a power function of body size and exponentially with temperature, thereby treating the effects of body size and temperature independently. Mounting evidence shows that the scaling of metabolic rate with body mass itself depends on temperature. Across-species analyses in fishes suggest that the mass-scaling exponent decreases with increasing temperature. However, whether this relationship holds at the within-species level has rarely been tested. Here, we re-analyse data on the metabolic rates of four freshwater fish species, two coregonids and two cyprinids, that cover wide ranges of body masses and their naturally experienced temperatures. We show that the standard metabolic rate of the coregonids is best fit when accounting for a linear temperature dependence of the scaling of metabolic rate with body mass, whereas a constant mass-scaling exponent is supported in case of the cyprinids. Our study shows that phenotypic responses to temperature can result in temperature-dependent scaling relationships at the species level and that these responses differ between taxa. Together with previous findings, these results indicate that evolutionarily adaptive and phenotypically plastic responses to temperature affect the scaling of metabolic rate with body mass in fishes.

Metabolism constitutes a fundamental property of all animals and plants as it supplies an organism with energy and materials from its environment. The most important factors influencing the metabolic rate are body mass and temperature. In poikilotherms whose body temperature varies along with that of the environment, metabolism links the ambient temperature to intrinsic physiological processes. This interaction between environment and individual metabolism affects ecological and evolutionary processes at all levels of organization. It has been argued that in aerobic eukaryotes body mass and temperature, through the effects on metabolism, explain most of the variation in fecundity and mortality (Savage et al. 2004), determine rates of biomass production and population growth (Brown et al. 2004), and control the overall rate of molecular evolution (Gillooly et al. 2005). These processes are closely linked to individual metabolism, because metabolism determines the rates of resource uptake and resource allocation to growth and reproduction. Understanding the effects of body mass and temperature on the metabolic rate is thus of major importance in ecological and evolutionary theory.

The metabolic rate (R) of an organism is typically expressed as a power function of body mass (M) according to $R = R_0 M^b$, where R_0 and b are the scaling coefficient and exponent, or intercept and slope of the log-log plot of metabolic rate against body mass, respectively. While the scaling coefficient varies considerably between species and taxa, the scaling exponent was consistently found close to 0.75 in the early works by Kleiber (1932, 1947). However, others argued that an exponent of 0.67 would constitute a general rule (Rubner 1883, Brody 1945, Heusner 1982), and some meta-analyses have reported broad ranges of experimentally determined values (e.g. 0.4–1.3, Clarke and Johnston 1999). Derived from physicochemical constraints on energy and material transport, West et al. (1997, 1999) suggested that the ¾ power constitutes a universal scaling relationship in living organisms. The metabolic theory of ecology (MTE) was later developed to link the metabolic rate of an organism to its body mass and body temperature (Gillooly et al. 2001, Brown et al. 2004). Gillooly et al. (2001) showed that the metabolic rate of all organisms could be approximated by $R = R_0 M^b e^{((E_i (T - T_0)) / kTT_0)}$, where T is absolute temperature (K), k is the Boltzmann constant (eV K^{-1}), and E_i is the activation energy for the rate-limiting biochemical reactions. Setting the reference temperature T_0 to the freezing point of water (273.15 K) defines $(T–T_0)$ as temperature in degrees Celsius (°C). The exponential temperature component of the equation, derived from the application of statistical thermodynamics to whole-organism metabolism, was termed the 'universal temperature dependence of metabolism' (UTD) (Gillooly et al. 2001, 2006, Allen and Gillooly 2007).

The claims of universality of the mass dependence (¾ power law) as well as the temperature dependence (UTD) have been criticized for various theoretical and empirical reasons (Dodds et al. 2001, Bokma 2004, Clarke 2004,

2006, Glazier 2005, Nagy 2005, O'Connor et al. 2007, White et al. 2007, Packard 2009). Alternative theories have recently received increasing attention, such as the metabolic level boundaries (MLB) hypothesis, which states that the range of possible metabolic states is defined by physiological 'boundary' constraints, resulting in scaling exponents of 0.67 to 1.0 (Glazier 2005, 2010). Today, there is mounting evidence that the mass-scaling exponent shows considerable variation intra- and interspecifically (Caruso et al. 2010, Clarke et al. 2010, Isaac and Carbone 2010, Kolokotrones et al. 2010, White 2010), and that it varies according to ecological factors (Glazier 2010, Killen et al. 2010). Glazier (2005) showed that ectothermic vertebrates generally exhibit higher interspecific scaling exponents than endothermic vertebrates and that the effect of temperature on the metabolic scaling may vary among species. In a recently published meta-analysis, Killen et al. (2010) compared the mass-scaling exponents (b) of 89 fish species by using one exponent per species that was measured close to the middle of the species' naturally experienced temperature range. Their study shows that the intraspecific scaling of metabolic rate with body mass decreases with increasing temperature across species. This relationship either reflects consistent phenotypic responses to environmental temperature across species, suggesting the same pattern at the within-species level, or it reflects species-specific adaptations to temperature, suggesting genetic differentiation as the underlying process.

Here, we investigate if the observed across-species relationship holds at the within-species level when the full range of naturally experienced temperatures is included in the analysis. We do this by comparing the intraspecific temperature dependence of metabolic scaling of four freshwater fish species, two coregonids, *Coregonus albula* and *Coregonus fontanae*, and two cyprinids, *Abramis brama* and *Rutilus rutilus*. Specifically, we test the alternative hypotheses of a temperature-independent and a temperature-dependent (linear or non-linear) scaling of the standard metabolic rate with body mass. By comparing two pairs of closely related and sympatrically occurring species, we study whether the temperature dependence of metabolic scaling is a phenotypically plastic or a genetically adaptive response to environmental temperature.

Methods

Species

The two coregonids (*Coregonus albula*, *C. fontanae*) occur sympatrically in Lake Stechlin, Germany. Both are highly active pelagic fishes that migrate vertically within the hypolimnion of the lake (Mehner et al. 2010a). The two cyprinids (*Abramis brama*, *Rutilus rutilus*) occur sympatrically in many European freshwaters (Mehner et al. 2007). These species are bentho-pelagic fishes that migrate predominantly horizontally in shallow waters between structured and open-water habitats. Coregonids are commonly found in cold-water and cyprinids in warm-water fish communities (Mehner et al. 2007). In both cases, fish that were used for the metabolic rate measurements originated from lakes in which the species occur sympatrically (the coregonids from Lake Stechlin and the cyprinids from Lake Belau, Germany).

Data

The metabolic rate data were taken from measurements of oxygen consumption rates during aerobic respiration of acclimated and starving fish at controlled temperature conditions. Methodological requirements for including respirometry data in our analysis were that 1) no individual fish was used in more than one experiment at one specific temperature, 2) stress-induced elevated respiration rates at the start of an experiment could be statistically excluded, and 3) spontaneous activity could be statistically excluded from the analysis. Careful consideration of data is important to avoid confounding effects when determining metabolic rate to temperature relationships (Irlich et al. 2009). Comparable data sets using this type of methodology and providing metabolic rate measurements over a wide range of body masses and temperatures were available for *C. albula* ($n = 42$; temperatures 4, 8, 15°C; mass range 10.2–75.0 g), *C. fontanae* ($n = 42$; temperatures: 4, 8, 15°C; mass range 3.6–37.4 g), *A. brama* ($n = 76$; temperatures 5, 10, 15, 20, 23°C; mass range 1.0–560.0 g), and *R. rutilus* ($n = 62$ temperatures 5, 10, 15, 20, 23°C; mass range 3.2–200.0 g) (data for cyprinids in Hölker 2003, 2006; data for coregonids in Ohlberger et al. 2007, 2008). All data were collected using long-term intermittent-flow respirometry. The temperatures investigated in the studies cover the full range of the species' naturally experienced temperatures (Hölker and Breckling 2002, Mehner et al. 2010a). Oxygen consumption of individual fish was measured in multiple measuring intervals for several hours. The acute oxygen consumption rate of the fish was computed by fitting a linear regression to the decrease in oxygen saturation against time for each measuring interval. Since fish initially show elevated oxygen consumption rates due to handling stress and changing conditions, data from the beginning of each trial were excluded from the analyses. Furthermore, to avoid the inclusion of elevated respiration rates due to spontaneous activity during the subsequent measurements, only the lowest 10% of those oxygen consumption rates were used to determine the minimum active metabolic rate at a given swimming speed (Hölker 2003, Ohlberger et al. 2007). The standard metabolic rate of the cyprinids was directly measured at 0.1 body lengths s^{-1}, whereas the standard metabolic rate of the coregonids was determined as the metabolic rate at zero speed by fitting a power function to the obtained minimum oxygen consumption rates at various speeds. Both procedures give reliable estimates of standard metabolic rates (Hölker 2003, Ohlberger et al. 2007). Hence, standard metabolic rate was determined as the metabolic rate at rest of an individual fish of a given body mass and at a given temperature. Several experiments ($n \geq 6$) were conducted at each of the 3–5 experimental temperatures and no individual fish was used in more than one experiment at one specific temperature. Other data sets using the same methodology and statistical analyses could not be identified in the literature. The metabolic rate data were used in their original, non log-transformed scale to avoid biased parameter estimates (Packard 2009, Caruso et al. 2010).

Models

The temperature and mass dependence of the standard metabolic rate was tested using the following three equations.

A temperature-independent scaling with body mass was described by the equation presented in Gillooly et al. (2001):

$$R = R_0 M^b e^{\left(\frac{E_i (T - T_0)}{kTT_0}\right)} \quad (1)$$

A temperature-dependent mass exponent was obtained by complementing the exponent b with a temperature term. This term either contained linear temperature dependence, as suggested by the relationship found across species presented in Killen et al. (2010):

$$R = R_0 M^{(b + c(T - T_0))} e^{\left(\frac{E_i (T - T_0)}{kTT_0}\right)} \quad (2)$$

or the scaling exponent was represented by an optimality function to allow for non-linear temperature dependencies:

$$R = R_0 M^{(b + c(T - T_0) + d(T - T_0)^2)} e^{\left(\frac{E_i (T - T_0)}{kTT_0}\right)} \quad (3)$$

where M is body mass (g), T is temperature (K), T_0 is temperature at the freezing point of water (273.15 K), k is the Boltzmann constant (eV K^{-1}), and E_i is activation energy (eV). The parameters R_0, b, c, d and E_i were estimated in a non-linear least-squares regression using the Gauss-Newton algorithm. E_i was estimated as it varies between species and was not known for the species studied (Vetter 1995, Gillooly et al. 2001).

Model selection was performed using likelihood ratio tests. We selected the best model in each species by pairwise comparison of the candidate models. A model was considered superior if the p-value of the likelihood ratio test was ≤ 0.05 (calculated using a χ^2 distribution). We first compared model 2 to model 1 and subsequently model 3 to the previously selected model. All analyses were performed using the statistical computing environment R (R Development Core Team 2008).

Results

The model that was best supported by the pairwise comparison based on likelihood ratio tests varied between species. Model 1, the one comprising a temperature-independent mass-scaling exponent, was the best model for *R. rutilus* and *A. brama* (Table 1). When using this model for the two cyprinids, all estimated parameters were statistically significant (Table 2). The estimated mass-scaling exponents (b) were close to ¾ power in both species, with values of 0.787 ± 0.041 and 0.718 ± 0.038 (estimate $\pm$ SE) in *A. brama* and *R. rutilus*, respectively. Estimates for the activation energy (E_i) were similar for the two species and within the previously reported range (0.2–1.2eV; Vetter 1995, Gillooly et al. 2001, Downs et al. 2008). The estimated normalization constant (R_0) was lower in *A. brama* compared to *R. rutilus* (Table 2). The resulting relationship between mass-scaling exponent and temperature is shown in Fig. 1A. When using model 2 or 3 for the cyprinids, estimates for the parameters a, c and d were statistically not significant (results not shown), supporting a temperature-independent mass-scaling exponent.

In contrast to the cyprinids, the model 2 comprising a linear temperature-dependence of the mass-scaling exponent was the best model for *C. albula* and *C. fontanae* (Table 1). In both cases, all parameter estimates were statistically significant (Table 3). The parameter estimates for the coefficient of the linear temperature term c within the mass-scaling exponent were significantly different from zero and identical in both coregonids (-0.020 ± 0.008), resulting in linearly decreasing mass exponents with increasing temperature. The estimated mass-scaling exponents b at a temperature of 0°C were 1.010 ± 0.105 and 0.903 ± 0.105 in *C. albula* and *C. fontanae*, respectively. Hence, at this temperature the standard metabolic rate is predicted to scale nearly isometrically with body mass. The relationship between mass-scaling exponent and temperature is shown in Fig. 1B. Estimates for the activation energy (E_i) did not differ between the coregonids, and were within the previously reported range (Vetter 1995, Gillooly et al. 2001, Downs et al. 2008). The normalization constant (R_0) did not differ between the coregonids, and tended to be higher than for the cyprinids (Table 2, 3). When using model 3, the estimates for the parameter d of the non-linear term were small and statistically not significant (results not shown), supporting a linear temperature dependence of the metabolic scaling. When using model 1 for the coregonids, all parameter estimates were significant and the mass exponent b was estimated at intermediate values (*C. albula*: 0.769 ± 0.035; *C. fontanae*: 0.659 ± 0.035).

Discussion

We find that the scaling of metabolic rate with body mass is temperature-independent in *A. brama* and *R. rutilus*, and temperature-dependent in *C. albula* and *C. fontanae*. Hence, the species-specific response to temperature was the same within, but different between the taxa. Our study demonstrates that the relationship of a decreasing mass-scaling exponent with increasing temperature found across species applies also at the within-species level in the coregonids, but not in the cyprinids. These findings suggest 1) that phenotypically plastic responses to

Table 1. Values of log-likelihoods (logL) for each model by species, ordered by the number of parameters (K). The given p-values for the pairwise model comparisons are based on likelihood ratio tests. Model 2 was first compared to model 1. Subsequently, model 3 was compared to the previously selected model (1 or 2). Based on this comparison, model 2 had most support in *C. albula* and *C. fontanae*, whereas model 1 had most support in *A. brama* and *R. rutilus*.

		C. albula		*C. fontanae*		*A. brama*		*R. rutilus*	
No.	k	logL	p-value	logL	p-value	logL	p-value	logL	p-value
1	3	–132.87		–96.09		–336.63		–216.86	
2	4	–129.61	0.0108	–92.93	0.0120	–336.28	0.4046	–216.84	0.8379
3	5	–129.60	0.8530	–92.91	0.8283	–335.20	0.2391	–216.21	0.5216

Table 2. Parameter estimates, standard errors (SE), *t*-values and p-values of the non-linear least-squares regressions according to model 1 (Table 1) in *A. brama* (DF = 73, n = 76) and *R. rutilus* (DF = 59, n = 62).

	A. brama				*R. rutilus*			
	Estimate	SE	*t*-value	p-value	Estimate	SE	*t*-value	p-value
R_0	0.348	0.092	3.754	<0.001	0.597	0.123	4.851	<0.001
b	0.787	0.041	19.296	<0.001	0.718	0.038	18.807	<0.001
E_i	0.641	0.037	17.466	<0.001	0.594	0.030	19.794	<0.001

temperature can result in temperature-dependent scaling relationships within species, 2) that the plastic responses to temperature differ between species or taxa and may depend on their ecology and evolutionary history, and 3) that both genotypic and phenotypic responses to temperature may affect the metabolic scaling.

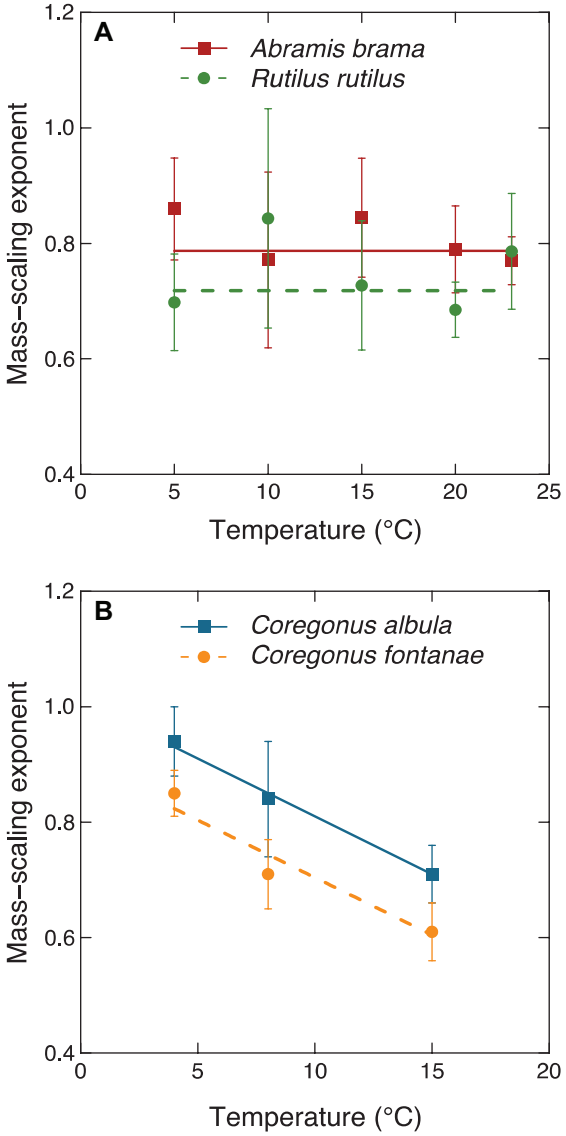

Figure 1. Predicted mass-scaling exponent versus temperature relationship (lines) within the naturally experienced temperature range in (A) *Abramis brama* (red squares and solid line) and *Rutilus rutilus* (green circles and dashed line) according to model (1) and (B) *Coregonus albula* (blue squares and solid line) and *Coregonus fontanae* (orange circles and dashed line) according to model (2). The parameter estimates of the mass-scaling exponent at each single temperature according to $R = R_0 M^b$ are indicated by circles (estimate) and vertical lines (standard error).

Recently published studies show that the scaling of metabolic rate with body mass varies considerably across species (Caruso et al. 2010, Clarke et al. 2010, Glazier 2010, Isaac and Carbone 2010, Kolokotrones et al. 2010, White 2010). Furthermore, it has been demonstrated that the scaling exponent varies systematically with respect to ecological factors (Glazier 2010, Killen et al. 2010). These findings conflict with the common view that species-specific differences or ecological factors only influence the elevation (or intercept) of the metabolic scaling relationships, but not the scaling exponent (or slope), which directly follows from a universally applied ¾-power (Glazier 2010). By taking one *b*-value per species and comparing across 89 fish species, Killen et al. (2010) showed that the scaling of metabolic rate with body mass decreased with increasing temperature across species. Here, we present a statistical modelling approach to test for such a relationship at the within-species level and apply this approach to four species for which the respective data were available (using the same experimental setup and protocol, see Methods). In the cyprinids, metabolic rate was well modelled using the equation given by the metabolic theory of ecology according to which body mass and temperature affect metabolism independently of each other, whereas in the coregonids the scaling of metabolic rate with mass was clearly temperature-dependent. This within-group consistency but between-group variation may be a result of the close phylogenetic relationship of the two coregonids on the one hand and the two cyprinids on the other hand (Mehner et al. 2010b, Kottelat and Freyhof 2007). This pattern could result from different phenotypic responses to temperature, perhaps related to the species' ecology, or alternatively their phylogeny, which may have lead to the evolutionary emergence of distinct phenotypes that either do or do not show the described plasticity in their responses to temperature.

The temperature-dependence of the metabolic scaling in coregonids may be explained by the recently developed metabolic level boundaries (MLB) hypothesis. The MLB hypothesis states that activity level and lifestyle influence the overall elevation of the metabolic rate to body mass relationship, which in turn influences the effect physical boundary constraints have on the slope of this relationship (Glazier 2010). It considers two idealized boundary constraints of the metabolic scaling relationship: 1) limits on fluxes of metabolic resources and heat across surfaces, which scale allometrically as $M^{0.67}$, and 2) limits on energy demand by tissues, which scale isometrically as $M^{1.0}$. The relative importance of these constraints depends on the metabolic or activity level. In resting organisms, metabolic scaling is expected to be primarily limited by fluxes of resources and heat across surfaces ($b \sim 0.67$) when

Table 3. Parameter estimates, standard errors (SE), *t*-values, and p-values of the non-linear least-squares regressions according to model 2 (Table 1) in *C. albula* (DF = 38, n = 42) and *C. fontanae* (DF = 38, n = 42).

	C. albula				*C. fontanae*			
	Estimate	SE	*t*-value	p-value	Estimate	SE	*t*-value	p-value
R_0	0.632	0.259	2.437	0.0196	0.630	0.213	2.955	0.0054
b	1.010	0.105	9.668	<0.001	0.903	0.105	8.568	<0.001
c	–0.020	0.008	–2.488	0.0174	–0.020	0.008	–2.492	0.0172
E_i	1.030	0.214	4.836	<0.001	1.090	0.171	6.393	<0.001

maintenance costs are high, whereas it is expected to be primarily limited by energy demand required to sustain tissues ($b \sim 1.0$) when maintenance costs are low. In general, cold temperatures are associated with lower maintenance costs than high temperatures due to the (exponential) temperature increase of metabolism, suggesting a decrease of the scaling exponent with temperature. Such a temperature effect on the scaling of standard metabolic rate with body mass was found for the two coregonids. The slope of the metabolic scaling relationship is predicted to decrease from 0.93 to 0.71 in *C. albula* and from 0.82 to 0.61 in *C. fontanae* as temperature increases from about 4°C to 15°C (temperature range

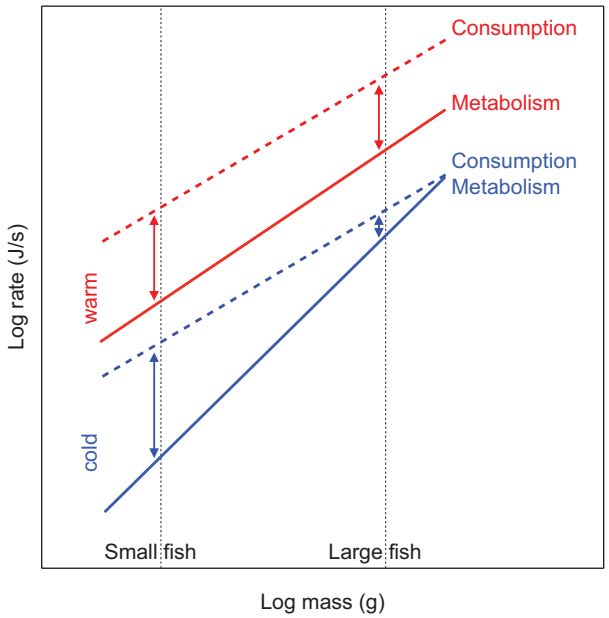

Figure 2. Schematic illustration of energetic consequences for small and large fish at different metabolic scaling relationships (slopes 0.67 and 1) while assuming constant allometric scaling of consumption. Slopes of metabolism were set to 1.0 at cold and 0.67 at warm temperatures (see MLB hypothesis, Glazier 2010). The slope for consumption was fixed at 0.6, an approximate value for freshwater fishes (Persson and De Roos 2006). The slopes of the log-log relationship of these rates versus body mass represent mass-scaling exponents. We assume that the elevation (intercept) of consumption increases with temperature to a similar degree as the one for metabolism (Huuskonen et al. 1998). At high temperature (red), the amount of surplus energy, that is, the difference between consumption and metabolism (length of arrows) is similar for all fish sizes. In contrast, at low temperature (blue) the energy gain for growth processes is less in large compared to small fish (lower intercept but steeper slope for metabolism).

measured in the experiments). The estimates are within the range reported for other fish species (0.4–1.3, Clarke and Johnston 1999). This observed shift most likely represents a plastic response of energy metabolism to the changing thermal conditions. The estimated decrease of the scaling exponent of $0.02°C^{-1}$ is more pronounced than the decrease of $0.006°C^{-1}$ found across species (Killen et al. 2010).

One can only speculate about a genetic contribution to the reported variation in the metabolic scaling. The systematic variation of the scaling exponent with temperature (Glazier 2005, 2010, Killen et al. 2010) suggests a potential role of selection in shaping the observed pattern across taxa. Our and previous findings indicate that both processes, evolutionary and plastic responses, may determine how metabolic rates and the scaling of metabolic rate with body mass depend on environmental temperature. The intraspecific mechanisms may differ from those at the interspecific level and it has been suggested that some estimates of across-species comparisons are biased by high variability at the species level (Glazier 2005). Future research is needed to clarify the relative importance of genetic versus phenotypically plastic variation for species or taxon-specific differences in the temperature dependence of metabolic scaling.

Previously published single-species studies have also reported significant effects of environmental temperature on the slope of metabolic scaling within species. For instance, a negative temperature effect was found in the white-spotted lizard (*Acanthodactylus schmidti*, Al-Sadoon and Abdo 1991), as well as the southern catfish (*Silurus meridionalis*, Xie and Sun 1990). However, an extensive review of the available literature by Glazier (2005) showed that the intraspecific effect of temperature varies considerably between species. The krill *Euphausia pacifica*, for example, shows no significant temperature effect (Paranjape 1967), but a positive effect was found for the marine gastropod *Littorina littorea* (Newell 1973). The ultimate reason for different patterns of within-species scaling relationships remains speculative and further studies addressing species-specific responses to temperature are required to help explain the observed variation.

Potential ecological consequences of a mass-scaling exponent that varies with temperature are changes in intraspecific competition strength between differently sized individuals. This is because the relative competitive abilities of the size classes within a population largely depend on the scaling relationships of the physiological rates, most importantly metabolism and consumption. For example, if metabolic rate increases considerably faster with body size than the ability to consume and digest food, small individuals are expected to be competitively superior compared to larger ones (Persson et al. 1998,

Persson and De Roos 2006). In this case, large fish may suffer from starvation due to the increased energy requirements from metabolism compared to the energy uptake through consumption. It has been suggested that such asymmetrical competition between small and large fish, in which recruits outcompete larger individuals, can lead to oscillating population dynamics during periods of low food abundance in coregonids (Hamrin and Persson 1996). Our study suggests that the competitive superiority of small compared to large individuals may be more pronounced at lower temperatures in these cold-water fishes, as illustrated schematically in Fig. 2. In contrast, a competitive advantage of small fish at warm temperatures may occur if the scaling exponent for consumption is lower at warm temperatures, such as found for bream (*A. brama*) (Hölker 2000) and perch (*Perca fluviatilis*) (Ohlberger et al. 2011). Differences in size-dependent competition may thus be related to the species' thermal habitats. Our finding of a temperature-dependent metabolic scaling relationship indicates that competitive interactions between size-classes within a population depend on environmental temperature. This may have consequences for the size-structure and dynamics of natural populations that have not yet been considered in population ecology.

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