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RESEARCH ARTICLE

Oxygen consumption of the semi-terrestrial crab *Pachygrapsus marmoratus* in relation to body mass and temperature: an information theory approach

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Abstract *Pachygrapsus marmoratus* is a semi-terrestrial crab and the most common grapsid crab in the intertidal belt of rocky shores throughout the Mediterranean Sea, Black Sea and northeastern Atlantic. In this study, the combined effects of temperature (T), body mass (M), and sex (S) on the routine oxygen consumption rate (R) in *P. marmoratus* were quantified. The blotted wet body mass of the specimens ranged between 43 mg and 18.0 g, and five test temperatures were used between 13.5 and 28.0°C. Six candidate models that reflected different assumptions regarding the dependence of R on S and T were compared. Model selection was based on Kullback–Leibler's information theory and Akaike's information criterion (AIC). The model$R = \mathrm{e}^{A-E/BT_\mathrm{a}}M^b$ had the highest support by the data (E is the activation energy, $B = 8.618 \times 10^{-5}$ eV K^{-1} is Boltzmann's constant, T_a is the absolute temperature in Kelvin, and b the allometric scaling exponent); for *P. marmoratus* it was found that $R(\mathrm{mg\,h^{-1}}) = \mathrm{e}^{10.25-0.298/BT_\mathrm{a}}M^{0.754}$. No sex dependence of R was supported by the data. Following a multi-model inference (MMI) approach, the mean (± SE) allometric exponent $\hat{\bar{b}}$ was 0.750 (± 0.013) having a 95% (bootstrap) confidence interval of 0.726–0.774. Thus, it was established that *P. marmoratus* follows Kleiber's 3/4 law, as seems to be generally true for intertidal crabs. The allometric exponent was independent of temperature as has also been reported for many other marine invertebrates (at normal temperatures). Q_{10} values were relatively low, indicating wide thermal tolerance of the species. Model selection based on information theory is recommended for respiration studies, as an effective method in finding a parsimonious approximating model. MMI by model averaging, based on Akaike weights, is an effective way to make robust parameter estimations and deal with model selection uncertainty.

Introduction

The Grapsidae family is one of the richest among the Decapoda, in terms of intertidal species. *Pachygrapsus marmoratus* Fabricius is the most common grapsid crab in the intertidal belt of rocky shores throughout the Mediterranean Sea, Black Sea and northeastern Atlantic from Brittany to Morocco including the Canary Islands, the Azores and Madeira (Ingle 1980; Cannicci et al. 1999). *P. marmoratus* exhibits a semi-terrestrial lifestyle and is an omnivore that actively searches for food, relying on the intertidal community throughout its post-larval life (Cannicci et al. 2002). It is active for long periods of time both above and under the water (Cannicci et al. 1999) and has a high physiological plasticity in relation to the respiratory medium (De Pirro et al. 1999). *P. marmoratus* may also inhabit rock pools with rapidly changing environmental conditions.

Oxygen consumption rates (R) have been reported for several grapsid crabs, e.g., *Cyclograpsus lavauxi* (Innes et al. 1986), *Helice crassa* (Hawkins et al. 1982),

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Metopograpsus messor (Eshky et al. 1996), *P. crassipes* (Roberts 1957a; 1957b), and *P. marmoratus* (Houlihan and Innes 1984). For *P. marmoratus*, Houlihan and Innes (1984) studied the cost of walking and compared *R* in air and in seawater at two temperatures (20 and 30°C). Among the exogenous and endogenous factors that influence *R*, temperature (*T*) and body mass (*M*) are of great importance (Rao and Bullock 1954; Bertalanffy 1957; Kinne 1970; Gillooly et al. 2001). The purpose of the present study was to evaluate the combined effects of *T* and *M* on routine *R* in *P. marmoratus*, for the entire seawater temperature range in which the species is encountered and for the entire body mass range observed during ontogeny, with the exception of the larval stages (i.e., after benthic settlement). Routine *R* is defined as the oxygen consumption rate measured during uncontrolled but minimal activity.

In the past 20 years, modern statistical science has been moving away from traditional formal methodologies based on statistical hypothesis testing. In particular, traditional approaches of hypothesis testing when applied to model selection have often been found to be mediocre and of limited value (Akaike 1981) and it is suggested that its application will diminish in future (Burnham and Anderson 2002). Hypothesis testing schemes are based on arbitrary *a* levels (commonly 0.05 or 0.01), and multiple testing and tests between models that are not nested are problematic. The adjusted coefficient of multiple determination (R^2) that is often used in model selection was found to be a very poor approach (McQuarrie and Tsai 1998).

Model selection based on information theory is a relatively new paradigm in biological sciences and is quite different from the usual methods based on null hypothesis testing (Burnham and Anderson 2002). According to the information theory approach, data analysis is assumed to be the integrated process of a priori specification of a set of candidate models (based on the science of the problem), model selection based on the principle of parsimony, and the estimation of parameters and their precision. The principle of parsimony implies the selection of a model with the smallest possible number of parameters for adequate representation of the data, a bias versus variance tradeoff. Furthermore, rather than estimating parameters from only the 'best' model, parameters can be estimated from several or even all the models considered. This procedure is termed multi-model inference (MMI) and has several theoretical and practical advantages (Burnham and Anderson 2002).

In this article, model selection and MMI based on an information theory approach, was applied to models of oxygen consumption rate in relation to temperature, body mass, and sex, for *P. marmoratus*.

Materials and methods

Collection and handling of experimental animals

Crabs were collected by hand from the rocky coast of Saronikos Gulf (37°30′N–37°55′N; 23°E–24°E), from January to November 2005. Immediately after collection the animals were placed in 40-l plastic holding tanks, equipped with portable air pumps, and within 2 h were transferred to the laboratory. A total of 107 crabs were used in this study (52 males and 55 females).

Each crab was placed in a separate 18-l, 12-l or 5-l holding tank (depending on its size), filled with natural seawater of 38.5 ± 0.3 psu. Each tank had an undergravel biological filter for nitrification, with smashed coral as a medium (~2 mm diameter), and the water was oxygenated with an air-stone connected to an air-pump. Salinity was regulated daily by adding deionized water. Once a week, 50% of the water was renewed. A photoperiod of 12L:12D was maintained; the light period was between 0800 and 2000 hours. A plastic tube (of ~10 cm length and variable diameter depending on the size of the crab) was provided to each crab for shelter. The crabs were fed once a day ad libitum with frozen squid (*Loligo vulgaris*) and green algae (*Ulva* sp.).

Respiration measurements

Three constant-temperature chambers were used to regulate the temperature of the holding tanks. Experiments were performed at five test temperatures (13.5, 16.5, 20.0, 24.0, and 28.0°C), which cover the annual local range of coastal sea temperatures in the Saronicos Gulf (~13.5°C in winter and up to 28.0°C in summer). The initial incubation temperature did not differ by >2°C from the collection water temperature, to avoid thermal stress. Then, the temperature was gradually regulated to the chosen experimental temperature with a rate <1°C day^{-1}. The incubation temperature did not differ by >5°C from the collection water temperature; thus, the experiments at the low temperatures (13.5 and 16.5°C) were conducted during spring and winter months, the experiments at the high temperatures (24.0 and 28.0°C) during summer and early autumn and the 20°C series during late autumn. At the chosen experimental temperature, crabs were acclimated for more than a month, before the respiration measurements began. No females near spawning, spent females, crabs just before or after moulting, or crabs that did not feed regularly were measured. Measurements were always conducted in the morning (between 0900 and 1300 hours) and feeding time was always between 1400 and 1500 hours.

R measurements were carried out using closed chamber respirometry. Respiration chambers with a seawater volume of 2.0, 1.5, 1.0, 0.5, or 0.1 l were used, depending on the size of the crab; the body mass per unit volume of respiration chamber was always kept below 9 g l^{-1}. After their placement in the respiration chambers, crabs were left for ~30 min to calm down before the initiation of dissolved oxygen measurements; excessively mobile crabs in the respiration chambers were excluded from measurements. Dissolved oxygen was measured with a WTW (Wissenschaftlich-Technische Werkstatten) polarographic oxygen probe (Cellox 325) connected to a WTW (MultiLine P4) meter. One measurement was taken from each chamber every 30 min for a total period of 4 h; if oxygen concentration in the chamber fell below 4.0 mg l^{-1}, then the experiment was terminated earlier. A respiration chamber of the same volume, but with no crab, was used as a control, and exactly the same procedure was followed.

A time series (from 0 to 4 h) of the oxygen content of the chamber was calculated from the product of the oxygen concentration measurements and the chamber volume. The declining rate of oxygen content was calculated as the slope of the least squares line that fitted the data. The same was done for the control, and the oxygen consumption rate (*R*) of the crab was calculated as the difference between the two slopes (experimental tank—control). In this way, the potential contribution of bacterial respiration was taken into account. To check the linearity assumption, a residual analysis was conducted. If the oxygen content did not fall linearly with time, then the specific *R*-measurement was excluded, because *R* could not be considered constant; such was the case in <8% of the trials. For each crab, *R* measurements were performed twice on two successive days and the mean of the two replicate values was taken as the specimen's *R*. The body mass of each crab (*M*) was measured just after the second measurement; the crab was blot-dried and weighed (balance precision was 0.1 mg). In larger crabs sex was identified from the abdominal shape, while in smaller crabs from examination of the pleopods under a dissecting microscope.

Data analysis: candidate models

The dependence of *R* on body mass *M* is typically characterized by an allometric function of the form $R = R_0 M^b$, where *b* is the scaling exponent and R_0 a temperature dependent parameter that is characteristic of the kind of organism (West et al. 1997). To estimate the parameters of the allometric scaling law, least squares linear regressions were calculated on the ln-transformed *R* versus ln-transformed *M*. The general equations were of the form (Zeuthen 1953; Bertalanffy 1957):

$$\ln R = a + b \cdot \ln M, \tag{1}$$

where $a = \ln R_0$.

Several assumptions were made regarding parameters *b* and *a*, expressed in six candidate models (Table 1). Assuming that both parameters were temperature dependent but with no assumption on the functional form of this dependence, Eq. 1 was fitted to the data, separately for each temperature and five different pairs of *b* and *a* values were estimated (model g_1). Model g_2 assumed that the allometric scaling exponent *b* was independent of temperature and that only *a* was temperature dependent but again with no assumption on the functional form of this dependence. According to Gillooly et al. (2001) temperature governs metabolism through its effects on biochemical reaction rates, and this dependence is well approximated by the relationship

$$R_0 = c \cdot e^{-E/BT_a}, \tag{2}$$

where *E* is the activation energy, $B = 8.618 \cdot 10^{-5}$ eV K^{-1} is Boltzmann's constant (eV = electron volt, i.e., the energy required to move one electron through a potential difference of 1 V) and T_a is the absolute temperature (in Kelvin).

Combining Eqs.1 and 2, we have

$$\ln R = \ln R_0 + b \ln M = A - \frac{E}{BT_a} + b \ln M, \tag{3}$$

where $A = \ln c$. Equation 3 was fitted with non-linear least squares and constituted model g_3. In models g_1, g_2 and g_3, it was assumed that the model parameters were independent of sex. To check for sex dependence, the same assumptions as for models g_1, g_2, and g_3 were made jointly with the assumption of sex dependence and thus three extra models were formulated (g_4, g_5, and g_6 as in Table 1).

Table 1 The six candidate models used to describe the oxygen consumption rate R of *P. marmoratus* in relation to body mass M and temperature T

Model	Description	k
g_1	$\ln R = a_i + b_i \ln M,\ i = 1\ldots5$ A different set of intercepts a_i and slopes b_i for each test temperature; no sex dependence	11
g_2	$\ln R = a_i + b \ln M,\ i = 1\ldots5$ Different intercepts a_i for each test temperature but a common slope b; no sex dependence	7
g_3	$\ln R = A - E(BT_\mathrm{a})^{-1} + b \ln M$ No sex dependence	4
g_4	$\ln R = a_{ij} + b_{ij} \ln M,\ i = 1\ldots5,\ j = f, m$ Different intercepts a_{ij} and slopes b_{ij} for each test temperature and each sex	21
g_5	$\ln R = a_{ij} + b_j \ln M,\ i = 1\ldots5,\ j = f, m$ Different intercepts a_{ij} for each test temperature but a common slope b_j; different parameters for each sex	13
g_6	$\ln R = A_j - E_j(BT_\mathrm{a})^{-1} + b_j \ln M,\ j = f, m$ Different parameters for each sex	7

k is the total number of estimated regression parameters (including σ^2)

Information theory, model selection, MMI

The basis of the information theory approach to model selection and inference is Kullback–Leibler (K–L) information (or K–L distance), $I(f,g) = \int f(x) \log(f(x)/g(x|\theta))\,\mathrm{d}x$ (Kullback and Leibler 1951). $I(f, g)$ is the 'information' lost when model g (with parameters θ) is used to approximate full reality or truth f; equivalently $I(f, g)$ is interpreted as the distance from the approximating model to full reality (Burnham and Anderson 2002). Information theory proposes the minimization of K–L distance as a fundamental basis for model selection. However, K–L distance cannot be computed without knowledge of both full reality f and the parameters of every candidate model g. Akaike (1973) devised a method for approximating K–L distance, based on the empirical log-likelihood function. His method, Akaike's Information Criterion or AIC, is summarized in the formula $\mathrm{AIC} = -2\ln\left(\mathcal{L}(\hat\theta|\mathrm{data})\right) + 2K$, where $\ln\left(\mathcal{L}(\hat\theta|\mathrm{data})\right)$ is the numerical value of the log-likelihood (natural logarithm) at its maximum point and $\hat\theta$ is the vector of the model's estimated parameters.

The small-sample, bias-corrected form $\mathrm{AIC_c}$ (Hurvich and Tsai 1989) of the AIC (Akaike 1973; Burnham and Anderson 2002) was used for model selection. Specifically, $\mathrm{AIC_c} = \mathrm{AIC} + 2k(k+1)/(n-k-1)$, where for least squares $\mathrm{AIC} = n\ln(\hat\sigma^2) + 2k$, $\hat\sigma^2 = RSS/n$, RSS is the residual sum of squares, n the number of observations, and k is the total number of estimated regression parameters including σ^2 (i.e., k is the number of parameters in the model equation plus 1). Normally distributed deviations with constant variance were assumed. The model with the smallest $\mathrm{AIC_c}$ value ($\mathrm{AIC_{c,min}}$) was selected as the 'best' among the models tested. The $\mathrm{AIC_c}$ differences, $\Delta_i = \mathrm{AIC}_{\mathrm{c},i} - \mathrm{AIC_{c,min}}$ were computed over all candidate models g_i. According to Burnham and Anderson (2002), models with $\Delta_i > 10$ have essentially no support and might be omitted from further consideration, models with $\Delta_i < 2$ have substantial support, while there is considerably less support for models with $4 < \Delta_i < 7$. To quantify the plausibility of each model, given the data and the set of six models, the 'Akaike weight' w_i of each model was calculated, where $w_i = \exp(-0.5\Delta_i)/\sum_{j=1}^{6}\exp(-0.5\Delta_j)$. The 'Akaike weight' was considered as the weight of evidence in favor of model i being the actual best model of the available set of models (Akaike 1983; Buckland et al. 1997; Burnham and Anderson 2002). A residual analysis was conducted to check whether the results were consistent with the model assumptions.

Model averaged estimates were calculated by the formula

$$\hat{\bar{\theta}} = \sum_i w_i \hat\theta_i, \tag{4}$$

where $\hat{\bar{\theta}}$ denotes a model averaged estimate of parameter θ. The unconditional standard error of θ was estimated as (Burnham and Anderson 2002):

$$\mathrm{se}(\hat{\bar{\theta}}) = \sum_i w_i \left(\mathrm{var}(\hat\theta_i|g_i) + (\hat\theta_i - \hat{\bar{\theta}})^2\right)^{1/2}, \tag{5}$$

where $\mathrm{var}(\hat\theta_i|g_i)$ is the variance of θ according to model g_i, conditional on the model (i.e., assuming that model g_i is the 'true' model). Confidence intervals (95%) were estimated with bias corrected and accelerated bootstrap of the raw data, with bootstrap sample size $B_\mathrm{boot} = 10{,}000$ (Efron and Tibshirani 1993).

Results

A total of 107 R-values (from 214 measurements) were estimated at the five test temperatures using animals with body masses between 43 mg and 18.0 g (Table 2). As expected, R generally increased with T and M (Fig. 1). For each candidate model, the estimated parameters are given in Table 3 and the corresponding RSS, AIC$_c$, Δ_i, and w_i in Table 4.

The best model among the set of candidate models was g_3; g_2 was also substantially supported by the data. Models g_4 and g_5 had essentially no support, while models g_1 and g_6 had considerably less support than the best model. Interpreting Akaike weight w_i as posterior probability (i.e., given the data and the set of candidate models) that model i is the K–L best model, models g_3 and g_2 had a sum of weights = 96.4%; thus, a 95% confidence set for the K–L best model would include just these two models. Both these models assumed that the allometric exponent is not temperature dependent and that there is no sex dependence of R. Hence both assumptions on temperature dependence of b and sex dependence of R were falsified. The assumption on temperature dependence of b was made for models g_1 and g_4 that had a sum of Akaike weights of only 1.0%, while the assumption on sex dependence of R was made for models g_3, g_4, and g_5 where the sum of w_i was only 2.6%. For models g_2 and g_3, the residuals plotted against any independent variable or against the observed dependent variables showed no deviation from the constant variance assumption and the normal probability plots of the residuals were reasonably linear, indicating no substantial deviation from normality.

When a single model is not strongly supported (with $w_i \geq 90\%$) and competing models give alternative inferences, as is our case, MMI is recommended for more robust inferences (Burnham and Anderson 2002). Hence, the allometric exponent b was estimated by model averaging the corresponding estimated values from models g_2 and g_3. Equation 4 becomes $\hat{\bar{b}} = w_2^* \cdot \hat{b}_2 + w_3^* \cdot \hat{b}_3$, where $\hat{\bar{b}}$ denotes the model averaged estimation of the allometric exponent, $\hat{b}_2$ and $\hat{b}_3$ the estimations of the allometric exponent from models g_2 and g_3 respectively, and $w_i^* = w_i/(w_2 + w_3)$ $(i = 2, 3)$ are the rescaled Akaike weights ignoring the weight of all other models except g_2 and g_3. We found that $\hat{\bar{b}} = 0.750$.

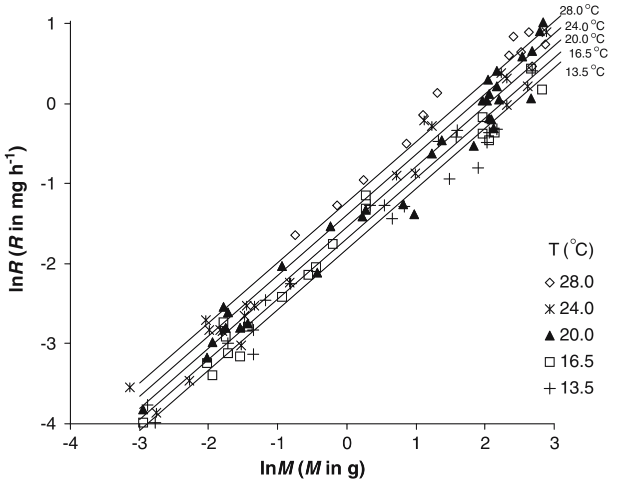

Fig. 1 *Pachygrapsus marmoratus*. Results of the oxygen consumption rate measurements (R) in relation to body mass (M) and temperature (T). Each point in the graph is the mean value of two measurements for a specimen, on consecutive days. R was measured in mg h^{-1} and M in g. Based on the 'best' model (g_3), regression lines were calculated for all five test temperatures

Table 2 Test temperatures (nominal value, mean and standard deviation) and sample size at each temperature

Test temperature (°C)			Number of specimens		
Nominal	Mean	Standard deviation	Total	Males	Females
13.5	13.57	0.32	21	11	10
16.5	16.68	0.17	20	10	10
20.0	20.24	0.43	33	14	19
24.0	23.73	0.44	21	11	10
28.0	28.00	0.20	12	6	6

Conditional standard errors and 95% confidence intervals (CI) were estimated for models g_2 and g_3 with bootstrap. For g_2, the standard error was$se(\hat{b}_2|g_2) = 0.0124$ and the 95% CI was (0.730, 0.778). For g_3, the standard error was $se(\hat{b}_3|g_3) = 0.0121$ and the 95% CI was (0.722, 0.769). The unconditional standard error of b was estimated from Eq. 5, with i taking only the values 2 and 3:

$$\begin{aligned} \mathrm{se}(\hat{\bar{b}}) = {} & w_2^* \cdot \left(\mathrm{var}(\hat{b}_2|g_2) + \left(\hat{b}_2 - \hat{\bar{b}}\right)^2\right)^{1/2} \\ & + w_3^* \cdot \left(\mathrm{var}(\hat{b}_3|g_3) + \left(\hat{b}_3 - \hat{\bar{b}}\right)^2\right)^{1/2} = 0.013. \end{aligned}$$

The 95% CI of the model averaged allometric exponent was estimated by bootstrapping the statistic$\hat{\bar{b}} = w_2^* \cdot \hat{b}_2 + w_3^* \cdot \hat{b}_3$ and was found to be (0.726, 0.774).

Activation energy was estimated to be, conditional on g_3, $\hat{E}_3 = 0.298$ eV. The standard error and 95% CI were estimated with bootstrap; the standard error was $\mathrm{se}(\hat{E}_3|g_3) = 0.036$ eV and the 95% CI was (0.228, 0.368) eV.

Table 3 *Pachygrapsus marmoratus*, the estimated regression parameters of the six candidate models g_i (as defined in Table 1)

Model	Parameters
g_1	$a_1 = -1.78$, $a_2 = -1.73$, $a_3 = -1.54$, $a_4 = -1.47$, $a_5 = -1.06$ $b_1 = 0.732$, $b_2 = 0.735$, $b_3 = 0.757$, $b_4 = 0.762$, $b_5 = 0.694$
g_2	$a_1 = -1.78$, $a_2 = -1.73$, $a_3 = -1.53$, $a_4 = -1.48$, $a_5 = -1.14$ $b = 0.746$
g_3	$A = 10.25$, $E = 0.298$, $b = 0.754$
g_4	$a_{1f} = -1.77$, $a_{2f} = -1.73$, $a_{3f} = -1.57$, $a_{4f} = -1.46$, $a_{5f} = -1.05$ $b_{1f} = 0.742$, $b_{2f} = 0.760$, $b_{3f} = 0.752$, $b_{4f} = 0.798$, $b_{5f} = 0.689$ $a_{1m} = -1.78$, $a_{2m} = -1.72$, $a_{3m} = -1.49$, $a_{4m} = -1.48$, $a_{5m} = -1.07$ $b_{1m} = 0.719$, $b_{2m} = 0.704$, $b_{3m} = 0.773$, $b_{4m} = 0.737$, $b_{5m} = 0.700$
g_5	$a_{1f} = -1.77$, $a_{2f} = -1.73$, $a_{3f} = -1.58$, $a_{4f} = -1.47$, $a_{5f} = -1.15$ $b_f = 0.756$ $a_{1m} = -1.79$, $a_{2m} = -1.72$, $a_{3m} = -1.47$, $a_{4m} = -1.48$, $a_{5m} = -1.13$ $b_m = 0.735$
g_6	$A_f = 9.65$, $E_f = 0.283$, $b_f = 0.761$ $A_m = 10.79$, $E_m = 0.312$, $b_m = 0.746$

Table 4 *Pachygrapsus marmoratus*, values of the residual sum of squares RSS, small-sample bias-corrected form of Akaike information criterion AIC_c, AIC_c differences (Δ_i), and Akaike weights w_i, for each of the candidate models

Model	RSS	AIC_c	Δ_i	w_i (%)
g_1	4.938	–0.69	7.77	1.0
g_2	5.036	–8.24	0.22	45.6
g_3	5.352	–8.46	0.00	50.8
g_4	4.722	22.63	31.09	0.0
g_5	4.928	4.23	12.69	0.1
g_6	5.316	–2.44	6.02	2.5

Based solely on the best model (g_3), the temperature dependence of R was estimated by the 'universal temperature dependence' (UTD):

$$\mathrm{UTD} = \exp(ET_c/BTT_0) = \exp\left\{ET_c/BT_0^2(1 + T_c/T_0)\right\}, \tag{6}$$

where temperatures are in Kelvin, T_0 is a reference temperature and $T_c = T - T_0$ (Gillooly et al. 2001). By choosing $T_0 = 273.15$ K (the freezing point of water), Eq. 6 expresses temperature dependence in terms of degrees Celsius, in which case T_c defines temperature in degrees Celsius. Thus, UTD was calculated from Eq. 6, as a function of temperature (in °C) (Fig. 2). Although UTD has advantages over the traditional Q_{10} factor (Gillooly et al. 2001), Q_{10} is widely used; thus, it was also calculated in order to compare our results with those of other studies. A Q_{10} value between a temperature T_c (in °C) and $T_0 = 273.15$ K, was calculated with the equation (Gillooly et al. 2001) $Q_{10} = \exp\left(10E/\left\{BT_0^2(1 + T_c/T_0)\right\}\right)$, when model g_3 was assumed, and is also given in Fig. 2. When model g_2 was assumed, Q_{10} was calculated as $Q_{10} = (R_{T_2}/R_{T1})^{10/T_2-T_1}$ and it ranged from 1.15, between 20.0 and 24.0 °C, to 2.22, between 24.0 and 28.0°C; the Q_{10} values are given for the consecutive pairs of test temperatures in Fig. 2 (dotted line segments).

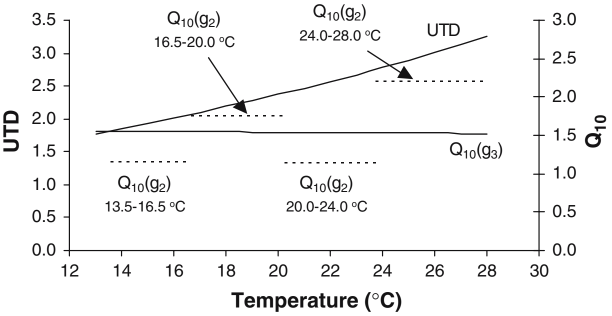

Fig. 2 *Pachygrapsus marmoratus*. Universal temperature dependence (UTD) and Q_{10} for oxygen consumption rates (R), as functions of temperature, based on model g_3 (*solid lines*). Q_{10} values between consecutive test temperatures are also given based on model g_2 (*dotted segments*)

Discussion

The relationship between the metabolic rates and body mass is a classic physiological issue that has been extensively discussed in the past. Kleiber (1932) argued that an animal's metabolic rate is proportional to its body mass raised to the power of 3/4, and this relationship was found to hold true for living organisms with size differences of more than 20 orders of magnitude. Bertalanffy (1957) distinguished three metabolic types according to the relationship between metabolic rate and body size. In the first type, the metabolic rate is proportional to a surface or the 2/3 power of the body mass ($b = 0.67$); in the second type, the metabolic rate is proportional to the body mass ($b = 1$); and, in the third type, the metabolic rate is intermediate between proportionality to body mass and proportionality to surface area ($0.67 < b < 1$). Recently, West et al. (1997) developed a general model that describes how essential materials are transported through space-filling fractal networks of branching tubes and derived Kleiber's 3/4-power scaling law. However, the West et al. (1997) theory has

Table 5 Allometric scaling exponents b of routine oxygen consumption rates in relation to body mass according to the relationship $R = R_0M^b$ and Q_{10} values (between temperatures T_1 and T_2) for intertidal crabs

Species	b (± SE)	Q_{10} (T_1–T_2)	Remarks	References
Cancer magister	0.576	1.54–4.10 (10–20°C)	4 life stages, 3 salinities	Brown and Terwilliger (1999)
Carcinus maenas	0.529	–		Newell et al. (1972)
Carcinus mediterraneus	0.597–0.815	1.4 (20–30°C)	Inactive and active animals	Houlihan and Innes (1984)
*Cleistosoma edwardsii**	–	1.4 (15–25°C)		Dye and Van Der Veen (1980)
*Cyclograpsus lavauxi**	0.84 (±0.21)	–	Non-ovigerous females	Taylor and Leelapiyanart (2001)
*Cyclograpsus lavauxi**	0.701	–		Innes et al. (1986)
*Helice crassa**	0.671	1.95, 2.06 (5–10°C) 2.01, 2.25 (10–15°C) 1.69, 1.39 (15–20°C)	For crabs of 50 and 200 mg dry tissue	Hawkins et al. (1982)
Heterozius rotundifrons	0.67 (±0.37)	–	Non-ovigerous females	Taylor and Leelapiyanart (2001)
*Leptograpsus variegatus**	0.854	–		Greenaway et al. (1992)
Macrophthalmus hirtipes	0.688	1.36 (5–10°C) 2.29 (10–15°C) 0.77 (15–20°C)		Hawkins et al. (1982)
Menippe mercenaria	0.86	–		Leffler (1973)
*Metopograpsus messor**	0.552	1.84 (15–20°C) 1.97 (20–25°C) 2.10 (25–30°C) 2.05 (30–35°C) 1.67 (35–40°C)		Eshky et al. (1996)
*P. crassipes**	0.664–0.730	2.66–3.04(8.5–23.5°C)		Roberts (1957a, b)
*P. marmoratus**	0.750 (±0.013)	1.52–1.56 (13.5–28°C)	Based on g_3	Present study
		1.17–2.22 (13.5–28°C)	Based on g_2	
*P. marmoratus**	0.410–0.654	1.4 (20–30°C)		Houlihan and Innes (1984)
Panopeus herbstii	0.8	–		Leffler (1973)
Pugettia producta	0.798	–		Weymouth et al. (1944)
*Sesarma catenata**	–	1.4 (15–25°C)		Dye and Van Der Veen (1980)
Uca inversa	0.574	2.52 (15–20°C) 3.17 (20–25°C) 2.81 (25–30°C) 2.42 (30–35°C) 4.82 (35–40°C)		Eshky et al. (1996)
Uca rapax	0.79	–		Vernberg (1959)
Uca pugnax	0.64–0.89	1.3–3.0 (14.8–24.5°C)	For two different latitudes	Teal (1959)

Only aquatic respiration was included and not R in air. When b did not differ significantly among different temperatures the common value was given otherwise the b-range. Standard errors (SE) of b were given when available. Grapsid crabs are marked with an asterisk

been criticized by many researchers, who question the initial assumptions (Whitfield 2001), while there are many examples in the literature of species that do not follow Kleiber's law, e.g., *Octopus vulgaris* (Katsanevakis et al. 2005). Dodds et al. (2001) re-analyzed published data sets dating back to Kleiber's original and concluded that the scaling exponents in most of them were statistically indistinguishable from 2/3. Darveau et al. (2002) presented a multiple-causes model of allometry, where the exponent b is the sum of the influences of multiple contributors to metabolism and control, which also supported the 3/4-power law for basal metabolic rate (but not for maximal metabolic rate). In *P. marmoratus*, we found $\hat{b} = 0.750$ and the corresponding 95% CI was (0.726, 0.774). Thus, it was established that *P. marmoratus* does follow Kleiber's law; the scaling exponent was significantly different from the value $b = 0.67$ and thus Bertalanffy's 2/3-power law was not supported.

Reported b values for intertidal crabs vary greatly from 0.41 to 0.89 (Table 5). A part of this variability should be attributed to the large sensitivity of b to several factors such as individual variability of routine R-measurements, sample size, and body mass range of the individuals measured. A very limited range of body masses is frequently responsible for wide variations in estimated b values, while small sample sizes may induce quite large standard errors in the estimation of b. For example, b was estimated for non-ovigerous female *Heterozius rotundifrons* and *Cyclograpsus lavauxi* by Taylor and Leelapiyanart (2001) with sample sizes $N = 18$ and 15, respectively; the corresponding standard errors were 0.37 and 0.21, respectively, which are much larger than the standard error of the present study (=0.013). Most of the reported b-values in Table 5 were estimated with rather small samples. Furthermore, most of the reported b-values did not include an estimation of precision and thus statistically meaningful comparisons of our *b* with values for other intertidal crabs were not possible. The mean of all reported *b*-values that we found in the literature was $b_{\mathrm{mean}} = 0.70$ with a 95% bootstrap CI (0.65, 0.75), indicating non-significant differences with the *b* found for *P. marmoratus* in this study.

For marine crustaceans, Zeuthen (1953) studied the increase in metabolism with phylogenetic increase in size and quoted an average value of 0.95 for sizes between 0.4 μg and 0.4 mg, and a value of 0.80 for sizes between 0.4 mg and 4 g. Scholander et al. (1953) found an average $b = 0.85$ for 15 tropical (at 30°C) and arctic (at 0°C) crustaceans. Weymouth et al. (1944) reported an average allometric exponent of 0.826 for 54 marine crustaceans ranging in size from 0.023 to 520 g. Thus, based on the results of this study and on Table 5, it is concluded that intertidal crabs seem to have allometric exponents slightly lower than the average for crustaceans in general.

For *P. marmoratus*, Houlihan and Innes (1984) reported a *b* value of 0.654 at 20°C and of 0.410 at 30°C. These *b* values are much lower than the estimated *b* of this study. However, as they do not give standard errors or raw data, we cannot statistically compare the two values. The range of body masses used in the present study was nearly twice that used by Houlihan and Innes (1984). The sample sizes in the latter study were also much smaller ($n = 11$ and 18 at two T) compared to this study ($n = 107$ measurement pairs). Thus, we consider the value of the present study more precise.

The assumption of temperature dependence of *b* was not supported by our data. This is in agreement with the results of several other studies on decapod Crustacea, e.g. for the semi-terrestrial crabs *Uca inversa* and *Metopograpsus messor* at six test temperatures between 15 and 40°C (Eshky et al. 1996), the fiddler crab *Uca urvillei* at five test temperatures between 15 and 30°C (Emmerson 1990), the shrimp *Xiphopenaeus kroyeri* at five test temperatures between 20 and 30°C (Carvalho and Phan 1997), and the shrimp *Penaeus monodon* at five test temperatures between 15 and 35°C (Kurmaly et al. 1989). Independence of *b* on temperature seems to be the rule in marine invertebrates when exposed to a normal range of temperatures and apart from crustaceans has also been reported for a variety of other organisms, e.g., in the common octopus *O. vulgaris* at six test temperatures between 13 and 28°C (Katsanevakis et al. 2005), and in the gastropod *Thais lapillus* at four test temperatures between 5 and 20°C (Stickle and Bayne 1982).

The dependence of the metabolic rate of *P. marmoratus* on temperature is contained in the term e^{-E_i/BT_a} of Eq.2. The E_i values should fall within the range of measured activation energies for metabolic reactions, which is between 0.2 and 1.2 eV, with an average of approximately 0.6 eV (Gillooly et al. 2001). Indeed, our estimations for E_i fell within this range. Most crustaceans have a Q_{10} between 2 and 3 (Wolvekamp and Waterman 1960). A Q_{10} close to 1 indicates thermal insensitivity, which has been interpreted as a mechanism by which energy could be conserved despite the increase in environmental temperature. *P. marmoratus* is a semi-terrestrial intertidal species that may also inhabit rock pools with extreme environmental conditions and thus the observed low Q_{10} is probably an adaptation due to its lifestyle and the wide range of temperatures encountered. Similar Q_{10} values have been reported for other grapsid crabs (Table 5).

The information theory approach frees the analyst from the limiting concept that the proper approximating model is somehow ‘given’. When a model is somehow ‘picked’, independent of the data, and used to approximate the data as a basis for inference, both the uncertainty associated with model selection and the benefits of selecting a parsimonious model are ignored. This strategy incurs substantial costs in terms of reliable inferences, because uncertainty in model selection is assumed to be zero. If model selection uncertainty is ignored, precision is often overestimated, estimated confidence intervals of the parameters are below the nominal level, and predictions are less accurate than expected. When the data support evidence of more than one model, model averaging the predicted response variable across models is advantageous in reaching a robust inference that is not conditional on a single model (Burnham and Anderson 2002). Under the information-theoretic approach it is not assumed that truth f is included in the set of models and the issue is not which model is true, but rather which model when fit to the data is the best one for representing the finite information contained in the data. The concept of a ‘true’ model seems to be of little utility in the biological sciences. Biological systems are quite complex with many small effects (tapering effects), individual heterogeneity, and interactions that are generally unknown. On an information-theoretic approach, ‘information’ about the biological system under study exists in the data and the goal is to express this information in a compact way; the more data available the more information exists, i.e., a more complicated model may approximate the data.

Conclusion

The relationship between the routine *R* and *M* in *P. marmoratus* followed Kleiber's law ($b = 0.75$), as seems to be generally true for intertidal crabs. The allometric exponent was independent of temperature as is rather the rule in marine invertebrates at normal temperatures, and the activation energy ($E_i = 0.3$ eV) fell within the normal range. Model selection based on information theory is recommended for respiration studies, as an effective method in finding a parsimonious approximating model. MMI by model averaging, based on Akaike weights, is recommended for making robust parameter estimations and dealing with model selection uncertainty.

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