Polar Biol (2012) 35:413–424
DOI 10.1007/s00300-011-1089-8

ORIGINAL PAPER

Metabolic rate and food availability of the Antarctic amphipod *Gondogeneia antarctica* (Chevreux 1906): seasonal variation in allometric scaling and temperature dependence

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Received: 30 May 2011 / Revised: 21 July 2011 / Accepted: 12 August 2011 / Published online: 1 September 2011

Abstract Among the few existing works on seasonal variation in metabolic rate of polar species, most have been conducted during summer due to logistic constraints and have been focused on species that cease feeding during winter. In this work, we present the first extensive data set on the seasonal variation in metabolic rate of *G. antarctica*, an abundant amphipod that feeds throughout the year, and its relationship with body size, potential food availability and temperature. We measured the resting metabolic rate (RMR) of groups of individuals during 6 months from late summer through winter at 4 experimental temperatures and for a wide range of body size. RMR had a negative allometric scaling with body size and showed a tendency to increase with temperature as expected. However, temperature and body size effects on RMR showed a significant temporal variation, and an increase in temperature decreased scaling exponents. RMR at the mean seawater temperature throughout the study showed a strong seasonal variation following food availability: RMR decreased from the end of summer through winter, coinciding with a reduction in microphytobenthos stock, but recovered summer values in August, when an epontic algae boom occurred. The seasonal factorial aerobic scope (×2.37) is lower than benthic Antarctic invertebrates that cease feeding during winter, in agreement with what is expected based on theoretical grounds. Results suggest that seasonal variation of RMR would allow *G. antarctica* to achieve a high efficiency in energy utilization, while maintaining the ability to exploit sudden changes in food supply.

Keywords Seasonal metabolism · Food availability · Amphipod · Microphytobenthos · Epontic algae

Introduction

Most Antarctic benthic marine invertebrates exhibit a seasonal cycle in activities such as feeding, growth and reproduction, with the highest rates occurring during summer (Brockington and Clarke 2001). While in temperate waters food availability and temperature vary throughout the year closely together, in the Antarctic marine environment, there is very little variation in seawater temperature and a much greater variation in food availability (Clarke 1988). The study of the seasonal variation in physiological rates of Antarctic marine species therefore offers the opportunity to research about the effect of a varying food supply with a relatively stable temperature across the year.

Metabolic rate and energy supply have been the center of debates concerning cold adaptations since the earliest studies on polar marine invertebrates (Peck 2002). The strong seasonality of high-latitude marine ecosystems makes the

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relationship between nutrition and metabolism of particular interest, since many polar organisms must survive long periods with a reduced or null food supply (Chapelle et al. 1994). Studies of seasonal variation in metabolic rate of marine polar species are important because they allow assessing the potential effect of food availability on species' energetic physiology. However, a few works on the seasonal variation in metabolic rate of polar marine organisms are available (Brockington and Peck 2001; Fraser et al. 2002; Obermüller et al. 2010; Obermüller et al. 2011), and most of the studies on the metabolic rate of marine Antarctic species have been conducted during the austral summer due to the logistic constraints of polar research.

The amphipod *Gondogeneia antarctica* is widely distributed along the western Antarctic Peninsula (WAP), where it is often one of the most abundant herbivores present in the shallow littoral benthic communities (Jazdzewski et al. 2001; Huang et al. 2007). This species occurs not only along the WAP, but is also found on the sub-Antarctic islands and in the Magellanic region (Richardson 1977). Its distribution occurs from the intertidal to 40 m depth in both soft- and hard-bottom benthic habitats, usually associated with abundant macroalgae (Thurston 1972; Jazdzewski et al. 2001; Huang et al. 2007). *G. antarctica* has two main spawning periods, with peaks at the end of February and at the end of September. On the other hand, the maximum life span of this species is 2.5–3 years, reaching adult weight usually within 1.5 years (Momo 1995). *G. antarctica* feeds mainly on benthic microalgae, but can also consume macroalgae, detritus and small amounts of microcrustaceans (Richardson and Whitaker 1979; Charles et al. 2005; Huang et al. 2006). In turn, the species is preyed by a large number of different species (e.g., Duarte and Moreno 1981; Creet et al. 1994; Fanta 1999; Barrera-Oro and Piacentino 2007; Barrera-Oro and Winter 2008).

Although *G. antarctica* plays a key role in the littoral food web of the WAP given its abundance and trophic position in the food web, little is known regarding the metabolic physiology of this species. There are only two published works that have measured the metabolic rate of *G. antarctica* (Opalinski and Sicinski 1995; Obermüller et al. 2007), but in both cases, only a small number of individual were measured on a single temperature and date. No data is currently available regarding the seasonal variation in the resting metabolic rate and its relationship with food availability, and the effects on metabolic rate of body size and short-term temperature variation are also unknown.

While many Antarctic benthic species do not feed for some periods during winter (Fraser et al. 2002 and references therein), *G. antarctica* is known to continue feeding throughout the year (Richardson and Whitaker 1979; Momo 1995). Clarke (1993, 2004, 2006) has formulated an evolutionary trade-off hypothesis, which states that the resting metabolic rate of any species at its normal environmental temperature is related with the maximum attainable metabolic rate and that there is therefore a trade-off between these metabolic traits. Whereas having a lower resting metabolic rate reduces energetic requirements to sustain life maintenance, a higher maximum metabolic rate would allow individuals to attain higher activity level such as feeding rates and thus a more efficient exploitation of varying resources. Clarke's evolutionary trade-off hypothesis allows deriving predictions of how metabolic rate will vary under a seasonal pattern of food availability: low resting metabolic rates will be associated with periods of a low food supply, and when food availability becomes high, a rise in resting metabolic rate will occur. When comparing species that feed throughout the year, such as *G. antarctica*, compared to species that cease feeding for some periods during winter (i.e., a low food availability period), seasonal variations in metabolism are expected to be of lesser extent in species that feeds throughout the year (Clarke 2004). Among works that studied seasonal variation in the metabolic rate of Antarctic marine invertebrates, most have focused on species that cease feeding to some extent during winter, and there are data available for only a few species that feed during the whole year (Fraser et al. 2002; Obermüller et al. 2010; Obermüller et al. 2011).

In this work, we present the first extensive data set on the seasonal variation in the metabolic rate of *G. antarctica* and its relationship with body size, food availability and temperature. The resting metabolic rate of groups of individuals was determined in the laboratory during 6 months from February to August of 1987 at 4 experimental temperatures for a wide range of body sizes. The objectives of this work were (1) to study the seasonal variation in the resting metabolic rate of *G. antarctica* from late summer till winter in relation to food availability and (2) to assess whether acute temperature dependence and metabolic scaling remains constant throughout this period of the year or are subject to temporal variation. We hypothesized that the seasonal variation in food availability produce a consequent variation in the resting metabolic rate of *G. antarctica* and that since *G. antarctica* feeds during the whole year, temporal variation in metabolic rate will be of lesser extent than in other species that do not feed during for some period of time during winter. The experimental results are discussed in the context of the ecology of the species, and implications for the energy expenditure are also considered.

Materials and methods

Study area

The study was conducted in Esperanza Bay (Fig. 1), on the north side of the Antarctic Peninsula (63°18′S–56°55′W),

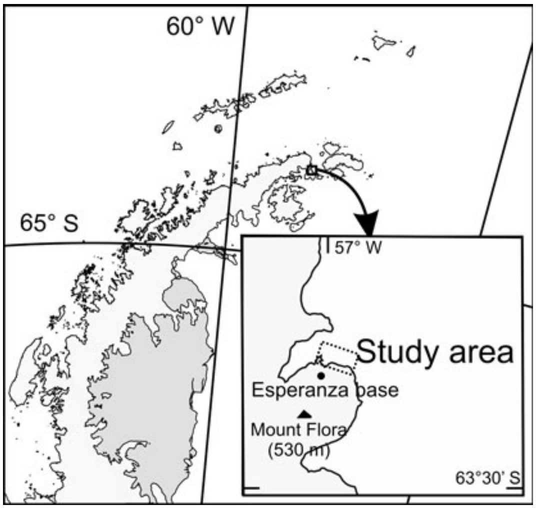

Fig. 1 Location of the study area

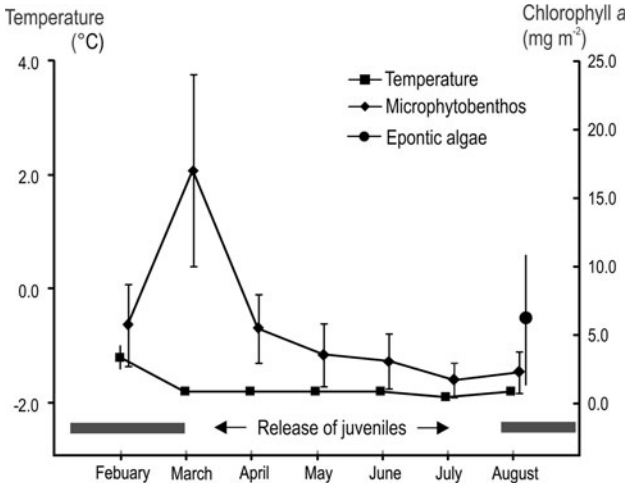

Fig. 2 Seasonal variation in food availability and temperature (mean ± SE) during the study period (modified from Brêthes et al. 1994). The periods when *G. antarctica* juveniles are liberated from females' brood pouch are also indicated

from February to August 1987. Water temperature is generally low due to the Weddell Sea surface water advection and ranged from −1.4°C in February to −1.8 ± 0.1°C during the rest of the survey (Fig. 2). Temperature was measured at 1 m depth with an YSI (model 59) oxygen-temperature probe when collecting animals for metabolic measurements at the last week of each month.

Collection of animals

Specimens of *G. antarctica* were sampled close to the shore at <1 m depth. A 300-μm mesh, hand zooplankton net was used to collect individuals. After collection, the animals were immediately transported to the laboratory in plastic containers filled with seawater for further experiments.

Metabolic measurements

Metabolic measurements were performed in the laboratory in February, and in April through August, at four experimental temperatures (−1.8 ± 0.2, 0.1 ± 0.2, 2.0 ± 0.1 and 4.0 ± 0.2°C), except in February and May, where the measurements at 2.0°C could not be performed due to the lack of a sufficient number of specimens obtained from the sampling site due to hard weather conditions at the time of experiments. The lowest experimental temperature (−1.8°C) was chosen in order to match the mean water temperature in autumn and winter in the natural habitat, which was only 0.4°C below water temperature in February.

The mean resting metabolic rate of groups of individuals with similar body size was determined by closed respirometry. The methodology was chosen given the low values of oxygen consumption obtained in preliminary measurements. The closed respirometry technique has been extensively used to conduct metabolic measurements on amphipods from various habitats (e.g., Chapelle et al. 1994; Wilhelm et al. 2006; Doyle and Momo 2009). After transportation to the laboratory, specimens were kept at the environmental temperature (−1.8°C), and under a constant low-illumination conditions, and starved for 24 h prior to metabolic measurements. Prior to metabolic measurements, individuals were subject to a period of physiological adjustment to experimental conditions for 8 h in the incubation chambers at the temperature at which metabolic measurements were performed.

The individuals used in the measurements included juvenile, immature and adult individuals of both sexes. Groups of specimens of similar body length were placed inside BOD bottles with a volume of 300 ml that were used as incubation chambers for metabolic measurements. The number of individuals of each group (5–20) was chosen according to body length, based on data obtained in preliminary metabolic measurements.

The incubation chambers were filled with Millipore HA (0.45 μm)-filtered seawater to avoid background oxygen consumption during measurements. Control measurements with no animals indicated that in these conditions no background oxygen consumption could be detected at the temperatures and incubation periods used. A small piece of 300-μm mesh net was placed inside each incubation chamber to provide a substratum to which amphipods could settle, as this showed to reduce activity of specimens in preliminary experiments, as reported in other works (e.g., Chapelle and Peck 1995; Spicer 1998). The prior assured that the actual resting metabolic rate was measured, i.e., metabolic rate of individuals with no locomotor activity.

Experiments for each date and temperature were performed in different animals and in different consecutive days at the last week of each month, in a random order. During measurements, water was maintained at the experimental temperature within ±0.1°C range, and incubation time lasted 6 h. At the end of measurements, incubation chambers were quickly inverted several times to ensure thorough mixing. Oxygen concentrations were determined with the aid of a polarographic dissolved oxygen meter model YSI 58 with a YSI 572 probe using high-sensitivity membranes, with a precision of ±0.1 mg O_2 l^{-1} and automatic temperature compensation for oxygen solubility. The oxygen meter was calibrated before each set of measurements for each temperature and date using the Winkler technique, a standard method for dissolved oxygen determination (Carpenter 1965). At the end of measurements, specimens were inspected to ensure that they were all alive; otherwise, data for that group was discarded. The initial seawater oxygen level was close to saturation, and during measurements, a maximum drop of 30% was allowed to assure individuals were not exposed to hypoxic conditions. Dry weight of the individuals was measured after drying the material 24 h at 105° and weighting on a laboratory balance with a precision of 10 µg. Specific resting metabolic rate of each group of specimens was calculated dividing resting metabolic rate by mean group dry body weight.

Benthic and epontic microalgae abundance

Potential food availability was estimated as the sum of benthic and epontic microalgae abundance, since *G. antarctica* is known to feed primarily on these two items, although as pointed out previously this is an omnivorous species (Richardson and Whitaker 1979; Huang et al. 2006). Microphytobenthos and epontic algae abundance existing at each date of sampling of *G. antarctica* for the experiments were previously published (Brêthes et al. 1994) and are shown in Fig. 2. Microphytobenthos sampling was done monthly at three depth levels (2, 5 and 10 m), while epontic algae were determined sampling the ice foot along the shore, and both were analyzed by standard methods to determine chlorophyll *a* concentration; methodological details are described in Brêthes et al. (1994) and references therein. Microphytobenthos abundance did not vary with depth, and therefore, standing stock of benthic and epontic algae was considered altogether to represent the potential food availability along the shore, where specimens of *G. antarctica* used in the metabolic measurements were obtained.

Data analysis

A full factorial general lineal model (GLM) was used to assess the dependence of metabolic rate with body size (dry weight) as continuous predictors and month of the year and temperature as categorical predictors. Temperature was treated as a categorical variable given that experiments were performed at 4 fixed experimental temperatures. Prior to analysis, body size (W) and resting metabolic rate (RMR) were log-transformed, since the expected relationship between the variables follows the power law $RMR = aW^b$, where b is the scaling exponents and a is a proportionality constant. The Q_{10} coefficient, which is the factorial change in metabolic rate with an increase in temperature normalized for a 10°C rise, was calculated as $Q_{10} = 10^{10.k}$, where k is obtained assuming an exponential relationship of metabolic rate with temperature: $\log_{10}RMR = c + k{\cdot}T$, with c being a proportionality constant. Statistical analyses were done using STATISTICA 8.0 (StatSoft Inc.) and R (R Development Core Team 2011). Data are expressed as mean ± standard error of the mean (SE), or otherwise indicated. Differences were considered significant at $P < 0.05$.

Experiments at 2.0°C could not be performed neither in February nor in May as previously described, therefore yielding a missing cells experimental design. As recommended in the statistical literature (Doncaster and Davey 2007), the whole data set as well as subsets representing complete designs was analyzed. Results of different analysis were consistent in all cases; therefore, results for the complete data set with missing cells are presented, and type II sum of squares were therefore used (Langsrud 2003; Doncaster and Davey 2007).

Best performance model was selected according to the second-order Akaike information criteria (AIC_c), which is recommended for a ratio of parameters to sample size <40 (Burnham and Anderson 2002). Model selection using the information-theoretic approach compare alternative models taking into account not only the variance explained by the model but also its complexity. This method also allows to avoid overfitting by achieving a proper trade-off between bias and variance, selecting thus more parsimonious models. Comparison between models is made using the difference between a model AIC and the lowest AIC, which correspond to the best model: a model with AIC Δ within 1–2 should receive consideration in making inferences; models having AIC Δ of 4–7 have considerably less support; and models with AIC $\Delta > 10$ have essentially no support and can be omitted from further consideration (Burnham and Anderson 2002).

The best performing model had a significant and large interaction term between temperature and month of the year, with qualitative distinctive effects for different dates. Consequently, to analyze the temporal variation in resting metabolic rate at the environmental temperature (−1.8°C), a separate GLM analysis was conducted considering only the measurements conducted at this temperature. In the results section, we therefore first present results obtained at the environmental temperature (−1.8 ± 0.1°C) and afterward show analysis for the whole data set including measurements at the other temperatures.

To evaluate the relationship of metabolic rate at the environmental temperature and potential food availability, we fitted linear models to describe changes in metabolic rate including intercept and/or potential food availability as predictors. The inverse of variance of metabolic rate means for each month were used as weighting factors, using as well the second-order Akaike information criteria (AIC$_c$) to compare model performance (Burnham and Anderson 2002).

Assumptions of the statistical analysis were evaluated to assess whether data could be properly analyzed with the proposed design. Plotting of residual of the statistical analysis in a QQ-normal probability plot (Doncaster and Davey 2007) showed that residuals had an approximately normal distribution, which was confirmed by a Kolmogorov–Smirnov test ($D_{239} = 0.063$, $P > 0.20$). Homogeneity of variance was assessed by the Levene test, which is recommended over other available tests (Lim and Loh 1996). Metabolic measurements performed at the environmental temperature from different months had homogeneous variance ($F_{5,66} = 1.14$, $P = 0.34$), but in the case of the other experimental temperatures, monthly measurements made at same temperatures differed in their variance ($P < 0.05$ in all cases). There was a small imbalance in the replication level between treatments (i.e., an experimental trial in a certain month at particular temperature), caused in part by the discard of data that did not satisfied the criteria regarding minimum oxygen levels at the end of the experiments. We tested whether data imbalance caused a loss of orthogonality between categorical predictors by performing correlation analysis between dummy variables for each level of both factors according to Hector et al. (2010), and results indicated that no spurious correlation among factor occurred due to unequal cell sizes.

It is well known that unbalanced data in the presence of variance heterogeneity can cause biased results. However, in the present data set, variance and cell number size were positively associated ($F_{2,20} = 6.47$, $P < 0.01$), and this situation in known to yield conservative results (Harwell 2003), with resulting P values being higher than actual values.

Results

The mean body size of individuals used in metabolic measurements was 5.57 mg dry weight (dw), with a range between 0.45 and 22.2 mg dw. The entire data set encompassed a total of 239 measurements, which comprehended a total of 3,479 individuals, with a mean number of 14.5 ± 4.1 animals per measurement. A similar number of measurements were performed for juveniles, immature and adult individuals.

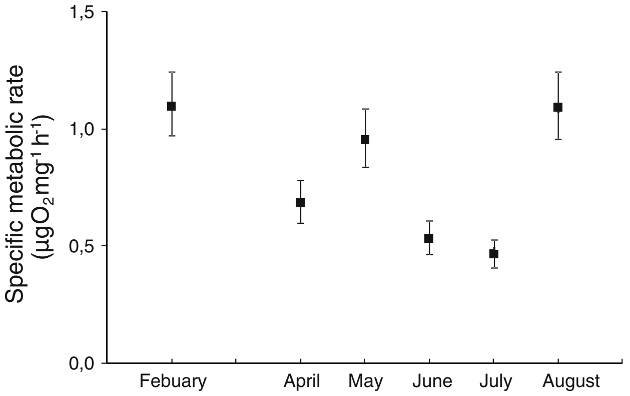

Fig. 3 Seasonal variation in the specific metabolic rate of *G. antarctica* at the environmental temperature (−1.8 ± 0.1°C). Plotted values are the least square means and 95% CI estimated by GLM analysis at the mean body size throughout measurements (3.5 mg dry weigh)

The specific resting metabolic rate of *G. antarctica* at the environmental temperature (−1.8 ± 0.2°C) ranged from 0.22 μg O_2 mg $^{-1}$ h^{-1} measured for individuals with a mean body size of 16.37 mg in July, to 2.22 μg O_2 mg $^{-1}$ h^{-1} for 0.90 mg individuals in February. The metabolic rate at the environmental temperature showed a strong seasonal variation ($F_{5,65} = 32.94$, $P < 0.001$), and along with body size, temporal variation accounted for 92.0% of the variance (adjusted $R^2 = 0.92$, $F_{6,65} = 137.38$, $P < 0.001$). Metabolic rates at the environmental temperature showed a decreasing trend from the end of the summer to winter, while recovering to values measured in February in August (Fig. 3). Minimum values were obtained in June–July, which were statistically similar but differed from all other months (Unequal N HSD, $P < 0.05$), and this temporal trend was similar regardless of the body size of individuals ($F_{5,60} = 1.88$, $P > 0.05$). The maximum seasonal factorial variation in metabolic rate was ×2.37, corresponding to the ratio of maximum values obtained in February and August to the minimum value registered in July.

A trend to higher metabolic rates with increasing potential food availability was observed (Fig. 4), but with a high degree of variability. In order to test whether temporal variation could be a response to a varying food availability, we examined the relationship between benthic and epontic microalgae along the shore and resting metabolic rate at the environmental temperature. The model with food availability alone was the model that performed better, followed by the null model including only the intercept (AIC$_c$ $\Delta = 0.75$), and the model with both variables (AIC$_c$ $\Delta = 5.0$), suggesting that food availability can account for temporal variation in metabolic rate at the environmental temperature. The initial decrease in metabolic rate from late summer to winter broadly followed the seasonal reduction in microphytobenthos stock (Fig. 2), and months with minimum seasonal values of metabolic rate (June–July) corresponded to

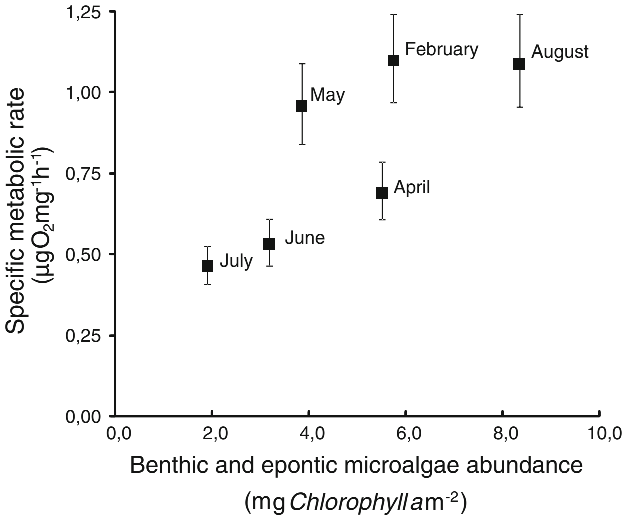

Fig. 4 Food availability and specific resting metabolic rate of *G. antarctica* at the environmental temperature, showing a trend of increasing values of metabolic rate with higher food availability. Plotted values are the least square means and 95% CI estimated by GLM analysis at the mean body size throughout measurements (3.5 mg dry weigh)

minimum values in food availability (Fig. 4). A sudden increase in resting metabolic rate occurred in August, and this coincided with the abrupt increment in food supply due to the epontic algae bloom (Fig. 2). To evaluate whether the inclusion of epontic algae stock affected the predictive power of food availability on seasonal metabolic rate, we reanalyzed the linear models with food availability including microphytobenthos stock alone. Indeed, excluding epontic algae made the model including food availability perform badly compared to the null model including only the mean metabolic rate value ($\mathrm{AIC_c}\ \Delta = 2.4$).

The best model for the whole data set of measurements at the four experimental temperatures provided a good fit to data, with 95% of the variance accounted for (adjusted $R^2 = 0.95$). The best model outperformed competing models by a large extent, with an $\mathrm{AIC_c}\ \Delta > 15.8$, and therefore other models are not further considered. The best performing model revealed a complex pattern of interactions between body size, temperature and month, and the results are summarized in Table 1.

The effect of temperature on metabolic rate differed between different size groups and varied over different months and seasons. An experimental increase in temperature with respect to the environment (−1.8°C) produced a highly variable effect on metabolic rate depending on the date of the year (Fig. 5). The interaction between temperature and time of the experiments accounted for more variation than both main effects of these factors (Table 1). The response of resting metabolic rate of *G. antarctica* to an increase in temperature showed a similar bell-shaped pattern from February through May, where an increase in temperature from −1.8 to 0.1°C increase metabolic rate from 20 to 64%, but a further increment in temperature did not increase or even decreased metabolic rate (Fig. 5). In June and July, maximum metabolic rates were obtained at 2.0 and 4.0°C, respectively. The most distinct pattern was observed in August, when an increase from environmental temperature (−1.8°C) produced a sharp decrease in metabolic rate, with values at 0.1 and 2.0°C being 50% of those at −1.8°C, followed by an increment at 4.0°C. The effect of temperature also varied with body size, with small individuals showing a greater increase in metabolic rate with temperature than bigger animals. The mean increase in metabolic rate with temperature was fitted by an exponential model in juvenile individuals (~1 mg dw), with an associated Q_{10} of 3.94 (2.40–6.47 CI 95), whereas in bigger specimens the fit of the exponential model was not significant. Immature individuals (~5.0 mg dw) had a mean Q_{10} of 3.71 (range: 0.93–6.60), while adults (~15 mg dw) presented a mean Q_{10} of 2.85 (0.67–5.2).

Table 1 Summary of results of the general lineal model on the effects of temporal variation, temperature and body size on the mean resting metabolic rate of *G. antarctica*

	Degrees of freedom	Sum of squares	*F* ratio	*P*
Body size ($\log_{10}$ dry weight)	1	16.8	3,086.6	<0.0001
Temperature	3	1.46	89.1	<0.0001
Month	5	1.09	40.1	<0.0001
Month × temperature	13	4.16	58.5	<0.0001
Month × body size	5	0.28	10.5	<0.0001
Temperature × body size	3	0.11	7.18	<0.001
Error	208	1.13		

The resting metabolic rate of *G. antarctica* showed a negative allometric scaling, with a mean scaling exponent of 0.62 ± 0.013, and accordingly, specific metabolic rate decreased with increasing body size with an exponent of -0.38 ± 0.013 ($F_{1,208} = 1{,}040.8$, $P < 0.0001$). However, since body size interacted with both date and temperature of experiments (Table 1), scaling exponents for a given month and temperature varied greatly, with a range of values from 0.41 to 0.84 considering the whole data set (Fig. 6).

Differences in the resting metabolic rate of different sized animals varied with temperature: at −1.8°C, a double in weight produced a mean increment of 62% in metabolic rate, while at 4.0°C doubling weight increased metabolic rate by 46%. An increase in temperature produced a decrease in scaling exponents, with a pattern that was well fitted by an inverse linear relationship (Fig. 7). Whereas a factorial increment of ×13 occurred at the environmental temperature considering the whole range of body size examined in this work (0.5 trough 20 mg dry weight), this

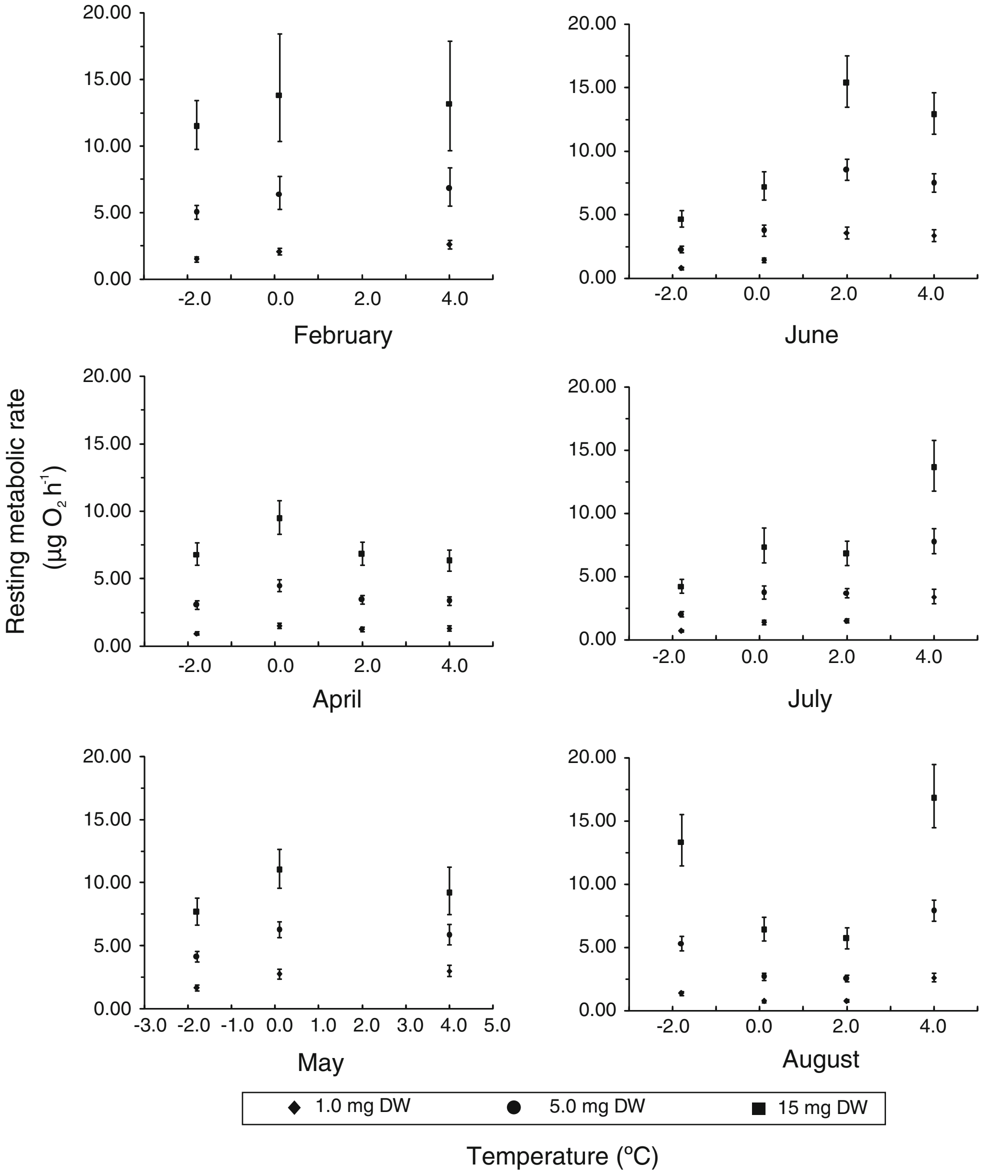

Fig. 5 Seasonal variation in the effect of temperature on metabolic rate of *G. antarctica* for three different body sizes, corresponding to juveniles, immature and adult individuals (1.0, 5.0 and 15.0 mg dw, respectively). Plotted data correspond to least square means and 95% CI estimated by GLM analysis

was reduced to ×7.5 when temperature increased to 4.0°C. Seasonal variation in scaling exponents, unlike the effect of temperature, followed no clear pattern. Lowest scaling exponents were obtained in May (0.49 ± 0.076), while maximum values were attained in August (0.77 ± 0.062).

Discussion

Seasonal variation in resting metabolic and food availability

The metabolic rate of *G. antarctica* at the environmental temperature showed a strong and similar seasonal variation in the whole body size range, showing that summer measurements cannot be extrapolated to winter months without incurring in great error. In the Antarctic marine environment, annual variations in temperature and production are uncoupled, and thus it is possible to distinguish the effects of one from the other (Clarke 1988). Seawater temperature at Esperanza Bay was relatively constant during the entire study period (Fig. 2), and therefore temporal variation found in the resting metabolic rate, as expected, could not be the effect of changes in seawater temperature.

Our results suggest seasonal variations in metabolic rates were related to food availability. The initial decrease in metabolic rate from late summer values broadly followed the seasonal reduction in microphytobenthos stock (Fig. 2),

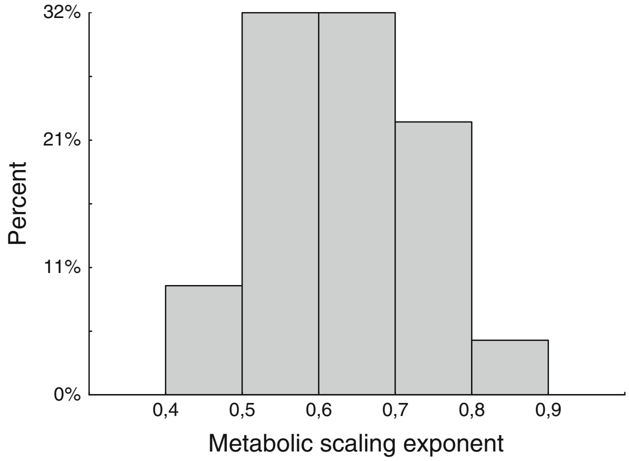

Fig. 6 Distribution of scaling exponents showing the amount of variation in metabolic scaling at different temperatures and time of the year ($n = 30$)

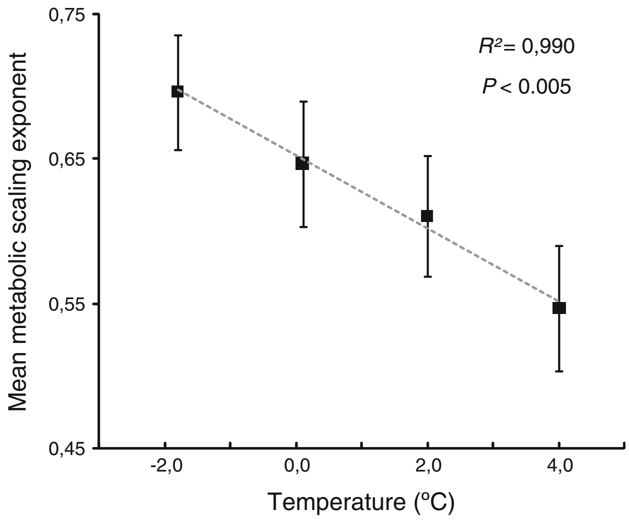

Fig. 7 Relationship between mean metabolic scaling exponents and temperature. R^2 and P-value correspond to the shown linear regression; *error bars* indicate 95% CI

with minimum values of metabolic rate obtained during periods with lower potential food availability. A sudden increase in metabolic rate occurred in August, and this coincided with the epontic algae bloom in the ice foot. Richardson and Whitaker (1979) reported the feeding of *G. antarctica* juveniles and adult individuals on microalgal flora of the ice foot at Signy Island at the end of the winter, and Momo (1995) reported a similar fact in Hope Bay. It is precisely during August when *G. antarctica* juveniles are released from females' marsupium, and these show a positive phototropism that direct them toward the ice, where epontic algae abound (Momo 1995). When epontic algae were excluded from the analysis, the predictive power of food availability on metabolic rate decreased. Our results thus support that epontic algae are an important resource for *G. antarctica* in a time of the year when other food sources are scarce.

The effect of food availability on the seasonal variation in the metabolic rate has been shown for several invertebrates of the Antarctic benthos (Brockington 2001; Brockington and Peck 2001; Fraser et al. 2002). While many Antarctic benthic species cease feeding in winter for periods ranging between a few weeks and several months (Fraser et al. 2002), *G. antarctica* feeds throughout the whole year (Richardson and Whitaker 1979; Momo 1995). We therefore expected that the seasonal factorial variation would be of less extent in *G. antarctica* than in species that ceases feeding during winter and thus depends exclusively on reserves to sustain life. The maximum seasonal factorial variation in metabolic rate of *G. antarctica* obtained in this study was ×2.4, a lower value than those reported for Antarctic benthic species that cease feeding in winter, with ×2.5–3.1 values reported in the echinoid *Sterechinus neumayeri* (Brockington and Peck 2001), and ×3 for the bivalve *Laternulla elliptica* (Brockington 2001).

The maximum seasonal factorial rise found in this study is higher than available data on other Antarctic benthic species that feed throughout the year. Obermüller et al. (2010) reported no clear seasonal pattern in the metabolic rate for *Paraceradocus miersii*, a gammariand amphipod with scavenger feeding habits. The reduced variability in the food supply of *P. miersii* from winter to summer is probably the cause of the lack of seasonality of metabolic rate in this species (Obermüller et al. 2010). A factor of 1.6× was reported for the limpet *Nacella concinna* (Fraser et al. 2002) that feeds mostly on microphytobenthos (Brêthes et al. 1994; Clarke 2008). Obermüller et al. (2011) suggest that *N. concinna* may exploit epontic algae. Whereas *N. concinna* and *G. antarctica* share microphytobenthos as food resource, a greater exploitation of epontic algae by *G. antarctica* might explain the increased seasonality of metabolic rate.

The relationship of resting metabolic rate and food availability found for *G. antarctica* is in agreement with the evolutionary trade-off hypothesis formulated by Clarke (2003, 2004, 2006), which states that a low metabolic rate implies a reduced energetic requirement, but on the other hand a higher metabolic rate, although energetically costly, allows a greater absolute aerobic scope and therefore more active lifestyles. The 2.4-fold increment in resting metabolic rate between July and August coinciding with the epontic algae bloom in the ice foot suggests a high metabolic plasticity of *G. antarctica*. A similar abrupt rise in metabolic rate with a sudden increase in food availability has been described for the Antarctic echinoid *Sterechinus neumayeri*, which increases its metabolic rate ×2.5–3 in only 1 month coinciding with the phytoplankton summer bloom (Brockington and Peck 2001). Such a rapid increase in the resting metabolic rate would allow individuals a better exploitation of the highly seasonal food supply. The low metabolic rates found in this study in June–July for *G. antarctica*, while abruptly recovering to rates similar to late summer when epontic algae become abundant, would allow this species to reduce its energetic demands during periods of low food availability. In contrast, the increase in resting metabolic rate when food availability increases would allow the species to attain higher maximum metabolic rates to acquire and process seasonal food sources as they become available. Interestingly, peaks in metabolic rate align with the periods when juveniles are liberated from females' brood pouch (Fig. 2), supporting the hypothesis that life history of *G. antarctica* is indeed coupled with energy supply as previously suggested by Momo (1995).

Microphytobenthos and epontic algae stock were included as potential food availability because these are known to be the main food resource for *G. antarctica* (Richardson and Whitaker 1979; Momo 1995). However, as an omnivorous species, other items not considered here might contribute to the seasonality of food availability for this species. Jazdzewski et al. (2001) suggested that abundance of *G. antarctica* was associated with the presence of detritus produced by the macroalgal community in the littoral area, which were maximum during April, based on a 1-year study in Admiralty Bay (King George Island). In the present study, however, metabolic rates at the environmental temperature of specimens collected in April had a somehow lower than expected value in relation to food availability for that month, but the moment of the peak of macroalgal detritus might have differed.

Response of resting metabolic rate to an acute increase in temperature

Seawater temperature in the shallow littoral in Esperanza Bay varies between −1.9 and −0.3°C across the year (Brêthes et al. 1994). The range of temperatures used in this work exceeded this range in >4°C, but no indication of inhibition of metabolism or increased mortality was found during acclimation periods or experimental measurements. *G. antarctica* is known to colonize and proliferate in the intertidal zone during the summer (Obermüller et al. 2007). The Antarctic intertidal zone is characterized by considerable higher daily temperature fluctuations, and high temperatures can be reached during the summer, with values up to 8°C registered in low-tide periods in King George Island (Abele et al. 1999). It is thus likely that *G. antarctica* can experience temperatures >4°C during the summer, and if so, the range of temperatures used in this study would be included in the naturally occurring one. It is well known that Antarctic ectotherms from intertidal areas are more temperature tolerant than strictly stenotherm species (Pörtner et al. 2007). Although no systematic study of the thermal tolerance is currently available, it thus seems logical that *G. antarctica* would have a more tolerant response to temperature than other non-tidal Antarctic benthic invertebrates.

The effect of temperature on the resting metabolic rate showed a strong temporal variation. August was the only month in which an increase from environmental temperature produced a decrease in resting metabolic rate (Fig. 5). It has been described that during the epontic algae bloom, individuals of *G. antarctica* that inhabits shallow waters with <20 m depth positively select the near ice microhabitat (Richardson and Whitaker 1979; Momo 1995). In addition, Richardson and Whitaker (1979) observed that juvenile individuals show a positive phototrophic response, causing a migration toward ice areas with abundant epontic algae. The decrease in metabolic rate with temperature observed in August could be thus explained by a positive selection of low, near-freezing water temperatures prevailing in ice microhabitats, where refuge from predation as well as abundant epontic algae is available (Richardson and Whitaker 1979). Further work is needed to clarify whether these patterns are robust and, if so, have an adaptive value.

The magnitude of the effect of temperature in *G. antarctica* also varied with body size. Juvenile individuals (∼1 mg dw) had an average exponential increase across the whole range of experimental temperatures ($Q_{10} = 3.9$), whereas bigger animals, although had a lower but similar mean Q_{10}, showed a higher variability in the response of metabolic rate with temperature. The Q_{10} values found in this study for the average effect of temperature on metabolic rate are in the range commonly cited for Antarctic benthic invertebrates (Peck 1989; Peck et al. 2002).

Scaling of metabolic rate with body size

The metabolic rate of *G. antarctica* showed a negative allometric scaling with body size. A high degree of variation in the metabolic scaling was found due to the seasonal variation in scaling exponents and its dependence with temperature (Fig. 6). The scaling exponents found in this work are within the values reported for intraspecific metabolic scaling in Antarctic amphipods (Opalinski and Sicinski 1995) and in amphipods in general (Musko et al. 1995; Normant et al. 2004a, b; Wilhelm et al. 2006).

We found that the metabolic scaling of *G. antarctica* was affected by temperature, and, furthermore, this interaction was well described by an inverse linear relationship (Fig. 7). The decrease in scaling exponents produced a smaller increment in metabolic rate with body size at higher temperature. A higher sensibility to temperature increase in bigger individuals due to greater oxygen supply limitation has been found in several species (Pörtner and Knust 2007).

The decrease in scaling exponents with an acute temperature rise could be thus caused by a limitation in oxygen supply in bigger animals, which would produce a lower metabolic rate than expected. As mentioned above, *G. antarctica* is known to abound in the intertidal zone during the summer, where temperatures as high as 8°C can be reached. Therefore, if oxygen supply limitation actually occurs in bigger body sizes with increasing temperature, it seems that it would not severely constraint survival at high temperatures at least on the short term or that a trade-off between high food supply in the intertidal and a suboptimal physiological condition exists.

Even though body size and temperature are generally considered to have independent effects on metabolic rate (e.g., Gillooly et al. 2001), a variation in scaling exponents with temperature is actually frequent when dealing whit intraspecific scaling and can show either a linear negative or positive response (see Glazier 2005 and references therein). Ivleva (1980) investigated the metabolic rate of Atlantic marine crustaceans at different environmental temperatures (19, 25 and 29°C) and found an inverse interspecific relationship between temperature and scaling exponent in the range. Although many theories regarding the origin of metabolic scaling have been proposed (e.g., West et al. 1997; Suarez et al. 2004; see Glazier 2005 for a review), potential interactive effects of body size and temperature have been not explored. Global warming has also been shown to have effects on the size structure of populations (Daufresne et al. 2009), and some of its effects have been linked to thermal sensitivity due to an oxygen supply limitation (Pörtner and Knust 2007). However, a framework integrating the interactive effects of body size and temperature has not been yet developed. Such a theoretical development would allow to derive predictions to be tested with data sets such as the one used in this work.

Comparison with previous data on the metabolic rate of *G. antarctica*

The values of resting metabolic rate obtained in this study are similar or lower than the limited data available from previous published studies on *G. antarctica*. Opalinski and Sicinski (1995) studied the metabolism of individuals at 1°C during the summer, and a metabolic rate of 1.83 ± 0.35 μg mg^{-1} h^{-1} is estimated for a 5-mg individual based on the equation provided in their work, 43% higher than our estimation for a similar individual and temperature in late summer (1.28 ± 0.10 μg mg^{-1} h^{-1}). The differences between our study and results of Opalinski and Sicinski might be due to the lack of substratum during metabolic measurements in their work, a situation which is known to increase spontaneous locomotion in amphipods (Chapelle and Peck 1995). Obermüller et al. (2007) measured metabolic rate of a reduced number of individuals (4) in relation to UV exposure, and control values at 0°C had a mean of 1.11 ± 0.41 μg mg^{-1} h^{-1}, close to 1.05 ± 0.06 μg mg^{-1} h^{-1} estimated by our work for similar sized individuals (9.74 mg) in late summer. Comparison of our work with previous results indicates that experimental conditions and techniques used in the present study allowed the measurement of metabolic rate on non-stressed individuals and thus confirming the estimation of the actual resting metabolic rate.

Conclusions

The strong seasonal variation in metabolic rate of *G. antarctica* from late summer through winter suggests that food availability is the main factor driving this temporal trend. The decrease in resting metabolic rate during winter months reduces the energy demand during periods of low food availability. The step increase in metabolic rate found in August coincides with the epontic algae bloom in the ice foot and supports the significance of this food source for *G. antarctica* suggested by previous studies. The decrease in resting metabolic rate of *G. antarctica* during periods with lowest food availability and its abrupt increment when new food source becomes available would allow to attain higher maximum metabolic rates to sustain a fast exploitation of the epontic algae. The seasonal variation in the metabolic rate found in this study would thus allow *G. antarctica* to achieve a high efficiency in energy utilization while maintaining the ability to exploit sudden changes in the food supply. The seasonal factorial aerobic scope of *G. antarctica* was lower than for available data for benthic Antarctic invertebrates that cease feeding during winter for some period, in agreement with theoretical grounds.

The results of this work represent the first extensive data set available on the metabolic rate of *G. antarctica* in relation to seasonal variation, food availability, body size and temperature from late summer trough winter in Antarctica. The extensive data set of metabolic measurements allowed us to explore the temporal variation in the effect of body size and temperature on metabolism, which is usually not possible in metabolic rate studies due to the restricted data available. Metabolic scaling and short-term temperature dependence, far from being constant, varied during the study period, showing a complex seasonal variation in the effect of body size and increasing temperature in metabolic rate of *G. antarctica*.

The strong seasonal variation found in the metabolic rate of *G. antarctica*, along with similar previous findings in the temporal variation in metabolism of polar marine species, suggests that seasonal changes in energy processing should indeed be considered in energy budget studies, since single-time determinations might introduce severe bias into whole year estimations. While seasonal variation in resting metabolic rate at the environmental temperature was in agreement with seasonality of food availability, further studies are needed to explore possible causes and consequences of the temporal variation in temperature and body size effects on metabolic rate.

Acknowledgments We are very grateful with Santiago de la Vega, who performed the experiments during the 1987 winter, as well as the personnel of the Argentinean station Esperanza for their logistic support during the field operations. We are also grateful to two anonymous referees for comments and suggestions that largely improved the manuscript. During this work, S.R.D. was supported by a fellowship from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). This research was funded by the Instituto Antártico Argentino and the Université du Québec à Rimouski, with grants to G.A.F and J.-C. B, respectively.

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