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Saving by freezing? Metabolic rates of *Adamussium colbecki* in a latitudinal context

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Abstract Standard metabolic rates of the endemic Antarctic scallop, *Adamussium colbecki* (Smith, 1902), were measured in austral summer and under simulated winter conditions. Average mass-specific metabolic rates were significantly different between "summer" (151.17 ± 45.06 µl O_2 g^{-1} h^{-1}) and "winter" (106.52 ± 39.65 µl O_2 g^{-1} h^{-1}) animals. The overall metabolic rates of *A. colbecki* are comparable to those of other Antarctic bivalve species, but well below those of temperate scallop species. Data for 24 scallop populations (13 species) from different latitudes give no evidence for elevated metabolic rates in *A. colbecki* as suggested by the concept of "metabolic cold adaptation". A world-wide comparison of metabolic rate and overall growth performance of scallops indicates that in the Antarctic scallop the energetic advantage of low basal metabolism does not counterbalance the disadvantage of the prolonged seasonal period of food shortage.

Introduction

Antarctic benthic invertebrates exhibit slow growth, low P/B ratios (Brey and Clarke 1993), prolonged longevity, low activity (Arntz et al. 1994) and low metabolic rates (e.g. Ralph and Maxwell 1977; Luxmoore 1984; Chapelle and Peck 1995; Ahn and Shim 1998). In high-latitude marine systems, food availability is strongly seasonal and spatially patchy, whereas the temperature dependence of biochemical processes causes a general slowdown of metabolism (Peck et al. 1997; Clarke 1998; Pörtner et al. 2000). Evolutionary adaptation to these conditions may follow two alternative pathways. On the one hand, animals may be selected for enhanced "endurance", i.e. the ability to survive prolonged periods without food by reducing metabolic activity and/or increasing metabolic efficiency compared to temperate animals. Consequently, comparatively more energy could be channelled into growth and reproduction (Crockett and Sidell 1990; Clarke 1991). On the other hand, evolution could tend towards comparatively higher metabolic rates to enable the animal to be more active, as assumed by the hypothesis of "metabolic cold adaptation" (Krogh 1916; Wohlschlag 1964; for review see Peck 2002). Consequently, comparatively less energy could be channelled into growth and reproduction (for a detailed discussion see Clarke 1983, 1991; Pörtner 2002a). Some studies have found evidence for metabolic cold adaptation in Antarctic fish (Wohlschlag 1964; Forster et al. 1987; Hardewig et al. 1998). Other studies in fish (Clarke and Johnston 1999) and invertebrates (Ivleva 1980; Luxmoore 1984; Peck and Conway 2000), however, could not confirm these findings. Only the latter two studies considered benthic organisms to a greater extent, but they compiled respiration data of a wide variety of taxa. Therefore, small differences in metabolic activity related to other factors than temperature may have been obscured by statistical "noise" owing to differences in body size, life history and ecology. Hence, we focussed our study on one single family, the Pectinidae, i.e. organisms with very similar body size, body shape, lifestyle and life-history features.

The endemic Antarctic scallop, *Adamussium colbecki* (Smith, 1902), is a common, abundant member of the Antarctic nearshore fauna, with a circumpolar distribution (Ralph and Maxwell 1977; Berkman 1990). Highest densities are found above 100 m water depth (Chiantore et al. 2001), but single animals have been reported from depths down to 1500 m (Dell 1990).

We measured standard metabolic rates and overall growth performance of *A. colbecki* and collected similar data from the literature referring to 23 scallop populations (12 species) from tropical to north polar habitats.

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Based on these data, we tried to answer two questions: (1) does the Antarctic scallop show any signs of metabolic adaptations specific to the Antarctic environment and (2) is, among scallops, living at constantly low temperatures energetically "cheaper"?

Materials and methods

Sampling and maintenance

Experimental specimens of *Adamussium colbecki* were collected in January and February 2000 from sites near the Italian Antarctic station "Terra Nova Bay" (74°41.9′S; 164°07.5′E) either by SCUBA diving or with a naturalist's dredge. In the Bay of Terra Nova (Ross Sea) *A. colbecki* is common between 5 and 80 m depth, with densities up to 60 ind. m^{-2} (Chiantore et al. 2001). Water temperatures range from +1°C in summer to –1.9°C in winter, salinity is always close to 34 psu and available food is up to 0.33 g C m^{-2} $ind.^{-1}$ in summer (Albertelli et al. 1998; Povero and Petrillo 2000).

After sampling, animals were immediately transported to the laboratory at the station and cleaned of epibionts using a toothbrush. Thereafter they were maintained in aerated flow-through aquaria at ambient temperature (0–0.5°C), salinity (34 psu) and seston levels under natural light regime until further experimental use. For winter oxygen-consumption measurements, 100 scallops were transported by plane to the Alfred Wegener Institute (AWI, Germany) at the end of February. They were maintained in cooled aquaria with recirculating seawater (0 ± 0.5°C, 33–34 psu) in a 12 h dimmed light:12 h dark daily light regime. Animals were fed twice a week by adding six Planktontabs (HOBBY, Dohse Aquaristik) dissolved in 500 ml water to each aquarium tank (0.01 g C m^{-2} $ind.^{-1}$ at each feeding day, approximately 3% of summer amount). No deaths occurred after an acclimation period of 4 weeks.

Measurement of metabolic activity

Oxygen consumption was taken as a proxy of total metabolic activity. Summer metabolism was measured at Terra Nova Bay station 5–20 days after collection. Winter metabolism was measured under simulated winter conditions in the laboratory at AWI. To obtain data as close as possible to standard (resting) metabolic rates, as defined by Bayne et al. (1976), animals were prepared as follows before measurements: (1) "summer"-animals were deprived of food for 3 days, "winter"-animals for 7 days prior to experiments in order to minimise the effects of specific dynamic action of feeding (Wieser and Medgysey 1990); (2) to avoid handling stress, scallops were allowed to accommodate for 24–36 h to the respiration chambers prior to the start of measurements (e.g. Chapelle and Peck 1995); and (3) during each measurement run, animals were monitored at least 15 min at the start, once or twice during and at the end of the run. Specimens that did not open their valves and protrude their tentacles in a manner similar to undisturbed scallops or that changed their position within one trial were disregarded. Thus, the measured rate approximated the sum of metabolic activities needed to keep the organism alive.

Respiration measurements were carried out using an intermittent flow-through system (Fig. 1), which combines the advantages of closed-chamber and flow-through systems (Forstner 1983). Respiration chambers were small Perspex cylinders with a movable lid to adjust chamber volume (50–600 ml) to animal size (for technical details see Gatti et al. 2002). Experimental temperature was maintained at 0 ± 0.3°C by placing the chambers in a water bath set in a jacketed container that was connected to a thermocirculator (Lauda RS 6 CP). Each experiment consisted of a number of subsequent measurement runs (closed-system stage). Each run started with fully oxygenated water (saturation close to 100%) and ended when oxygen saturation fell to 75%. Thereafter the water was renewed (flow-through system stage) and a new measurement run started. Each run lasted 2–5 h, depending on individual oxygen consumption, each animal went through two to four runs (maximum duration of one experiment was 24 h). During the closed-system stage water was continuously circulated between respiration chamber and measuring optode (Fig. 1) by MASTERFLEX peristaltic pumps (model 7521-40 with a pump head system model 7519-05). In each experiment six respiration chambers with only one scallop each (all of approximately the same size) and a control chamber (without scallop) were measured simultaneously.

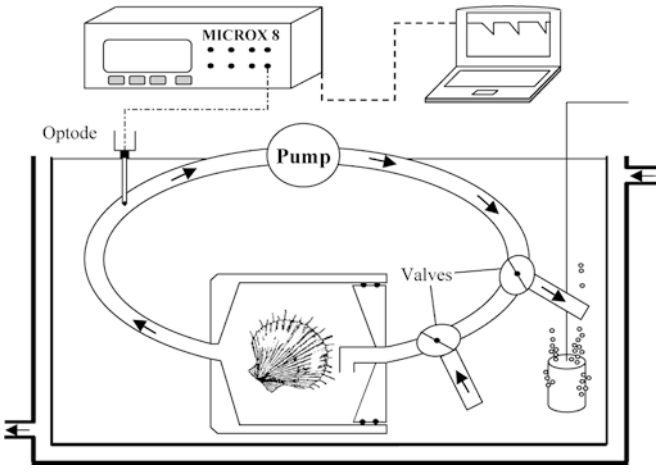

Fig. 1 Intermittent flow-through system for measurement of metabolic rates (flow-through stage with valves open displayed)

Oxygen content in the chambers was monitored continuously with oxygen microoptodes connected to a MICROX-8 array (PreSens, Neuweiler, Germany). The measuring principle of microoptodes is based on dynamic fluorescence quenching of an immobilised oxygen-sensitive fluorophor (for details see Klimant et al. 1995; for specific advantages of microoptodes for cold water oxygen measurements see Gatti et al. 2002).

Immediately after the end of each experiment, animals were dissected and soft tissue wet masses (WM) were determined to the nearest 0.1 mg after careful blotting with a paper. The tissues were frozen at −80°C for analysis of enzymatic activities (see Heilmayer et al. 2002). WM was converted to soft tissue dry mass (DM) by the conversion factor 0.159 obtained from a separate sample of 234 animals.

Calculation of metabolic rates

Metabolic rates (V_{O2}, in µmol O_2 $ind.^{-1}$ h^{-1}) were calculated from the slope of the oxygen evolution curve, after transforming the percent O_2 saturation to micromoles of dissolved oxygen in seawater using known values of oxygen solubility (Benson and Krause 1984) by:

$$VO_2 = \left(\frac{sat_0}{sat_{60}} \times 100\right) \times \alpha_{O_2} \times V_{Chamber} \quad (1)$$

where α_{O2} is the oxygen solubility in seawater (µmol dm^{-3}), $V_{Chamber}$ the volume of respiration chamber and tubing (dm^3), sat_0 the oxygen saturation (%) at the beginning of the experiment and sat_{60} the oxygen saturation (%) after 60 min as calculated from linear regression. Individual metabolic rates were corrected with the oxygen consumption of control chambers (no animal) and converted to millilitres O_2 by 44.66 µmol O_2 = 1 ml O_2 (Brey 2001). Metabolic rates were related to soft tissue DM by:

$$VO_2 = a \times DM^b \quad (2)$$

where a is a constant and b the scaling exponent. The model was fitted by least squares linear regression after logarithmic transformation of both variables.

Computation of standard metabolic rates (SMR)

To remove the effect of body mass (Luxmoore 1984; Packard and Boardman 1999) all oxygen data were converted to a standard animal size of 1 g dry mass (DM_S). For studies providing individual metabolic values (V_{O2}), individual standard metabolic rates (SMR_{ind}) could be calculated for each animal by:

$$SMR_{ind} = VO_2 \times (DM_S/DM_E)^b \quad (3)$$

where DM_E was the soft tissue dry mass of the experimental animal and b the mass exponent of the oxygen consumption–to–soft tissue dry mass relation (Kleiber 1975; Packard and Boardman 1999). For those studies that provided no individual data but only an overall allometric relationship between oxygen consumption and body mass for the whole population, population average standard metabolic rates (SMR_{avg}) as described by Luxmoore (1984) were computed by:

$$SMR_{avg} = a \times DM_{mean}^{b-0.807} \quad (4)$$

where a and b are the constants from the appropriate physiological function and DM_{mean} is the geometric mean dry mass determined from the mass range of the experimental data; 0.807 was the mean family-specific mass exponent determined in 81 studies with most values ranging between 0.7 and 0.9 (Heilmayer, unpublished data compilation).

Literature data constraints

Published data on the metabolic rates of other scallop populations were included in this study only if these data: (1) referred to inactive animals (i.e. resting metabolism), (2) were conducted in the normal temperature range of the species, and (3) covered a sufficient range of body mass values.

Statistical analysis

Hypothesis I: specific metabolic adaptations

To test whether Antarctic scallops exhibit metabolic adaptations specific to the Antarctic environment (H_A) or whether differences in the metabolism of Antarctic and non-Antarctic scallops are related to temperature only (H_0), we ran two analyses, one based on population average standard metabolic rates (SMR_{avg}) and one based on individual standard metabolic rates (SMR_{ind}). In both cases, an Arrhenius equation was fitted to the relationship between SMR and absolute temperature (T). Regarding SMR_{avg}, we checked whether the rates of *A. colbecki* were situated within the 95% confidence limits of the fitted Arrhenius model. Regarding SMR_{ind}, an ANCOVA [$\ln(SMR_{ind})$ versus "Antarctic↔non-Antarctic" and $1/T$] was applied.

Hypothesis II: investment in somatic growth

Energy spent on basal metabolism is ecologically "wasted" in the sense that it is not used for growth, reproduction or activity (for a detailed discussion see Parry 1983; Clarke 1987, 1991). Provided that all other parameters such as assimilation efficiency are independent of temperature, a reduced metabolic rate, as expected for *A. colbecki*, should point towards an enhanced ecological growth efficiency. To test whether Antarctic scallops invest comparatively more energy into somatic growth (H_A) or whether there is no difference to non-Antarctic scallops (H_0), we compared the ratio between somatic growth performance and SMR in *A. colbecki* and 12 non-Antarctic scallop populations. We used the "overall growth performance" (OGP) index P of Moreau et al. (1986) as a proxy of lifetime somatic growth performance (for more details Brey 2001):

$$P = \log(K + M_\infty) \quad (5)$$

where K and M_∞ are parameters of the von Bertalanffy growth function (VBGF). As the index P is proportional to the maximum rate of body mass increase during a lifetime (Pauly and Munro 1984), the SMR at the inflexion point of the growth model was used to calculate the P/SMR ratio. The residuals of the linear regression of P/SMR versus T were checked by ANOVA for significant deviation of the values referring to *A. colbecki*. As size–mass relations were not available for all 13 populations included, M_∞ was computed from H_∞ (mean asymptotic shell height, taken from the appropriate VBGF), and a common size–mass relation for scallops derived from 46 studies (Heilmayer, unpublished data compilation), such that:

$$\log(M_\infty) = -4.38 + 2.846 \times \log(H_\infty) \quad (6)$$

According to Feldman and McMahon (1983) this method is not expected to cause a statistical artefact.

Results

Adamussium colbecki measurements

The relation between body dry mass and shell height was not significantly different between summer and winter animals (ANCOVA of log-transformed data, $P = 0.4$) and can be described by the overall equations:

$$\begin{aligned} \text{'summer'}\ \log(DM) &= -5.862 + 3.446 \times \log(SH)\ (N = 89,\ r^2 = 0.944) \\ \text{'winter'}\ \log(DM) &= -6.634 + 3.749 \times \log(SH)\ (N = 14,\ r^2 = 0.955) \end{aligned} \quad (7)$$

Metabolic rates (V_{O2}) of summer animals varied between 7.81 and 751.41 µl animal^{-1} h^{-1} and were related to body mass by (Fig. 2a):

$$\log(VO_2) = 2.161 + 0.911 \times \log(DM)\ (N = 235,\ r^2 = 0.902,\ P < 0.001) \quad (8)$$

Winter metabolic rates ranged from 30.64 to 289.4 µl animal^{-1} h^{-1} and were related to body mass by (Fig. 2b):

$$\log(V_{O_2}) = 2.002 + 0.717 \times \log(DM)\ (N = 35,\ r^2 = 0.658,\ P < 0.001) \quad (9)$$

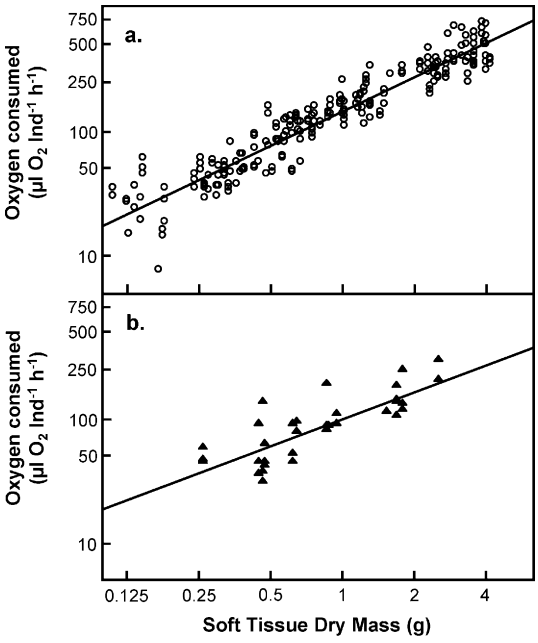

Fig. 2a, b *Adamussium colbecki*. Metabolic rates in relation to soft tissue dry mass. Regression lines shown were fitted by least-squares to logarithmically transformed data: Eqs. 8 and 9 for summer (*circles*) and winter (*triangles*), respectively

An ANCOVA (log metabolic rate vs. season, covariate log DM, only animals between 0.24 and 2.5 g DM, $P < 0.02$) showed that intercept (t-value = 175.86, $P < 0.001$) and slope (t-value = 21.13, $P < 0.001$) are significantly different. Metabolic rates of standard-sized *A. colbecki* (SMR_{ind}) in "summer" (151.17 ± 45.06 µl O_2 g^{-1} h^{-1}) were approximately 42% higher than in "winter" animals (106.52 ± 39.65 µl O_2 g^{-1} h^{-1}).

Metabolic rates in scallops

Population average standard metabolic rates (SMR_{avg}) of scallops are significantly and positively related to temperature, as indicated by the Arrhenius equation:

$$\ln(SMR_{avg}) = 30.011 - 8844.658 \times 1/T \quad (N = 80, 13 \text{ species}, r^2 = 0.714, P < 0.001) \quad (10)$$

Mean "summer" and "winter" values of *A. colbecki* were situated within the 95% confidence range of the model (Fig. 3a). ANCOVA of the individually measured standard metabolic rates (SMR_{ind}) (rate vs. Antarctic↔non-Antarctic, covariate $1/T$) provided no evidence for significant effects of the parameter "Antarctic" on metabolism ($F = 0.532$, $P > 0.1$). Hence, hypothesis I_A is rejected, and a common Arrhenius equation can be applied to the whole temperature range (Fig. 3b):

$$\ln(SMR_{ind}) = 13.397 - 4219.299 \times 1/T \quad (N = 936, 8 \text{ populations}, 6 \text{ species}, r^2 = 0.356) \quad (11)$$

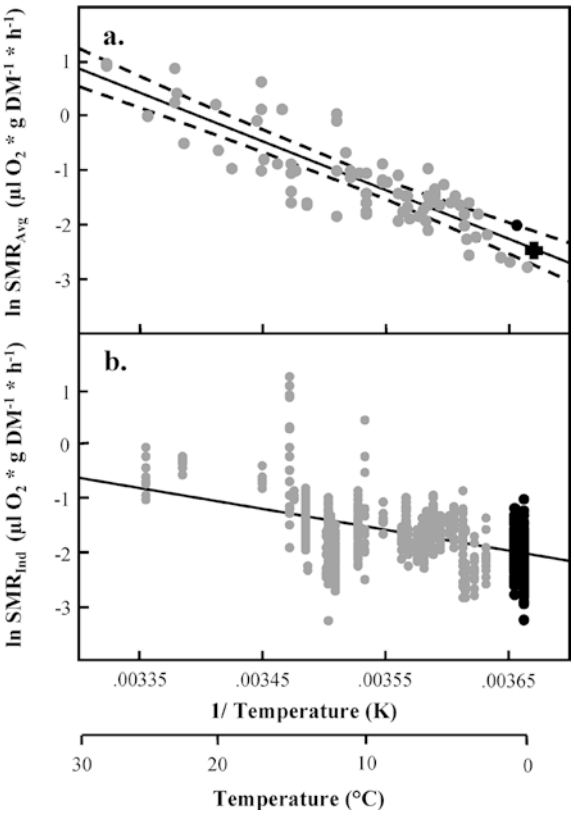

Fig. 3a Metabolic rates (µl O_2 g^{-1} h^{-1}) of scallop populations from different latitudes. Data presented are resting or standard rates for species at their normal ambient temperatures. Where seasonal data were available, more than one value is included. Species and references are as follows: *Aequipecten opercularis* (Vahl 1972; McLusky 1973; Heilmayer, unpublished data); *Argopecten circularis* (Silva Loera 1986), *Argopecten irradians concentricus* (Kirby-Smith 1972; Barber and Blake 1985; Yang et al. 1998a; Lu et al. 1999); *Argopecten irradians irradians* (Bricelj et al. 1987), *Chlamys deliculata* (Mackay and Shumway 1980); *Chlamys hastata* (Bernard and Noakes 1990); *Chlamys farreri* (Yang et al. 1998b); *Chlamys islandica* (Vahl 1978; Vahl and Sundet 1985; Schmid 1996); *Mimachlamys varia* (Shafee 1982); *Mizuhopecten yessoensis* (Fuji and Hashizume 1974); *Placopecten magellanicus* (MacDonald and Thompson 1986; Shumway et al. 1988; Grant and Cranford 1991; Pilditch and Grant 1999); *Zygochlamys patagonica* (Heilmayer et al. 2001); *Adamussium colbecki* (present study) (*black dot* summer animals; *black cross* winter animals). Arrhenius plot, with fitted least-squares regression line: Eq. 10. **b** Fitted Arrhenius model of the relationship between individual metabolic rate and temperature for eight populations of non-Antarctic and the Antarctic scallops: Eq. 11 [*grey dots* 666 data points, six scallop species (*Aequipecten opercularis*: McLusky 1973; Heilmayer et al. 2002; *Argopecten irradians irradians*: Bricelj et al. 1987; *Argopecten irradians concentricus*: Lu et al. 1999; *Chlamys islandica*: Vahl 1978; Vahl and Sundet 1985; *Mizuhopecten yessoensis*: Fuji and Hashizume 1974; *Zygochlamys patagonica*: Heilmayer et al. 2001); *black dots Adamussium colbecki* (present study)]

Metabolic investment in somatic growth

The ratio P/SMR is negatively related to temperature, i.e. the share of somatic growth in total metabolism decreases with increasing temperature (Fig. 4):

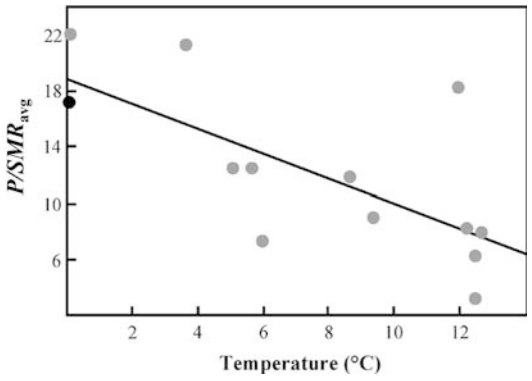

Fig. 4 Relationship of the ratio between standard metabolic rate (SMR_{avg}) and overall growth performance (P) to ambient temperature in 13 scallop populations. Data presented are resting or standard rates at their normal ambient temperatures. Where seasonal data were available, the data were averaged over the whole year: *Aequipecten opercularis* (Vahl 1972; McLusky 1973; Heilmayer et al. 2002); *Chlamys islandica* (Vahl 1978; Vahl and Sundet 1985); *Mimachlamys varia* (Shafee 1982); *Mizuhopecten yessoensis* (Fuji and Hashizumu 1974); *Placopecten magellanicus* (MacDonald and Thompson 1986; Shumway et al. 1988); *Zygochlamys patagonica* (Heilmayer et al. 2001); *Adamussium colbecki* (present study). (Overall growth performance data were taken from an unpublished data compilation of O. Heilmayer). Regression line: Eq. 12

$$\mathrm{P/SMR_{avg}} = 19.425 - 0.943 \times T \quad (N = 13,\ 7\ \text{species},\ r^2 = 0.519,\ P < 0.001) \tag{12}$$

No significant additional regional effects were detected by ANCOVA ($P > 0.5$), i.e. hypothesis $\mathrm{II_A}$ is rejected.

Discussion and conclusion

Metabolism of *Adamussium colbecki*

Our results indicate that the metabolic activity of *A. colbecki* is significantly higher in "summer" than in "winter" (Fig. 2), as observed in many boreal bivalves (Bayne et al. 1976; Ansell et al. 1980; Bricelj et al. 1987; Shumway et al. 1988) as well as in Antarctic invertebrates (Peck et al. 1987; Brockington 2001; Brockington and Clarke 2001). A seasonal change in poikilotherm metabolism may be related to a variety of environmental parameters, of which temperature and food supply are assumed to be the most important ones. Regarding boreal bivalves, some investigations emphasise the significance of temperature effects (see e.g. Worrall et al. 1983; Thompson 1984), whereas others suggest that food supply plays a more important role (e.g. Vahl 1978; MacDonald and Bourne 1987; MacDonald and Thompson 1988). In sublittoral Antarctic environments the annual range in seawater temperature rarely exceeds 3°C, and hence the marked seasonality of food availability is supposed to be the major determinant of metabolic activity in Antarctic invertebrates (Clarke 1988; Brockington and Clarke 2001). Our experiments reflect these conditions, as temperature is about 0°C during both "summer" and "winter" measurements, whereas "winter" food supply is only 3% of measured "summer" values.

Both the intercept and the slope of the log–log body mass–to–metabolism relationship (Fig. 2) are significantly different between "summer" and "winter". The difference in the intercept (2.161 to 2.002) signifies an increase of up to 44% in "summer" metabolism across the whole body mass range. This difference in the intercept is likely to reflect either a seasonally induced change of environmental factors (food availability, light) or an endogenic metabolic cycle, which results, e.g. in reduced or atrophied digestive mechanisms (Clarke 1991; Brockington and Clark 2001). The significantly higher slope (i.e. the mass scaling exponent, 0.911 vs. 0.717) represents an additional increase in summer metabolism. We believe this additional part reflects active (somatic and gonad) growth, as it seems to scale almost linearly to body mass (Fig. 5; Jørgensen 1988). The absolute values should not be taken too seriously, because the different body mass ranges and animal numbers that the two regressions are based on may have caused slight aberrations, as indicated by the negative values below 1 g body mass. Identical patterns and similar differences of the mass scaling exponent (higher during the growing season, significantly lower in winter), however, were found in *Argopecten irradians irradians* (Bricelj et al. 1987), *Chlamys islandica* (Vahl 1978, 1981) and *Mizuhopecten yessoensis* (Fuji and Hashizume 1974). These observations support Wieser (1994) and Jørgensen (1988), who suggested that a mass scaling exponent of metabolism close to 1.0 reflects active growth, whereas exponents around 0.75 are indicative of maintenance metabolism only.

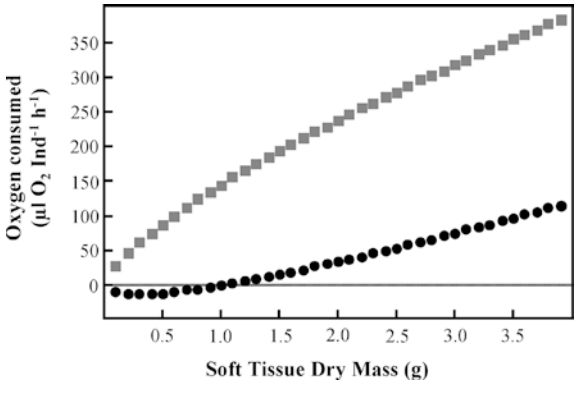

Fig. 5 *Adamussium colbecki*. A generalized model illustrating the relationship between body mass, "summer" maintenance metabolism (*squares*) and growth metabolism (*circles*) as calculated from the relation between respiration (V_{O2}) and body mass (DM) in "summer" and "winter" ["winter" total metabolism: $V_{O2} = 100.462 \times DM^{0.717}$, maintenance only, no growth; "summer" total metabolism: $V_{O2} = 144.877 \times DM^{0.911}$; "summer" maintenance metabolism: $V_{O2} = 144.877 \times DM^{0.717}$; "summer" active metabolism: $V_{O2} = 144.877 \times (DM^{0.911} - DM^{0.717})$]

Metabolism and temperature

Metabolic rates of *A. colbecki* are within the range reported for polar bivalve molluscs (Peck and Conway 2000), but among the lowest values reported for temperate and tropical scallops so far (Fig. 3a, b). Metabolism in bivalves is primarily a function of temperature, which can be described best by an Arrhenius model (Peck and Conway 2000). About 70% of the overall variation in population average standard metabolic rates (SMR_{avg}) are explained by temperature in our Arrhenius model (Fig. 3a). This is distinctly better than comparable models for fish (55–59%; Clarke and Johnston 1999) and bivalves in general (47%; Peck and Conway 2000). Obviously our more monophyletic approach reduces some lifestyle-related noise in the relation between metabolism and temperature. Different experimental setups, as well as differences in reproductive stage, may explain the remaining 30% variance. Neither the model based on SMR_{avg} data (Fig. 3a) nor the one based on SMR_{ind} data (Fig. 3b) provide any support for a significant elevation of the whole-organism metabolism of *A. colbecki* compared to non-Antarctic species. Hence, our study supports the conclusion of Clarke and Johnston (1999) and Peck and Conway (2000) that there is no "metabolic cold adaptation" (MCA, sensu Krogh 1916) on the level of organisms. Furthermore, neither metabolism nor animal behaviour gives any evidence for incomplete adaptation or "extra" savings, e.g. "hibernation" or failing response to stimulation (authors' personal observations). Like Ansell et al. (1998), we could not find any evidence for a reduced swimming performance in *A. colbecki* compared to temperate scallop species, although data for the maximum instantaneous capacities are not available so far.

It is generally accepted, however, that organisms inhabiting low temperature environments must have developed specific physiological adaptations at the cellular level (i.e. mitochondrial proliferation) to overcome the adverse effects of low temperatures on metabolism. This cellular MCA will, on the other hand, cause a rise in oxygen demand (e.g. Johnston et al. 1994, 1998; Clarke 1998; Somero et al. 1998; Pörtner et al. 2000; Pörtner 2002a, 2002b). The question arises at which organisational level those energy savings occur which counterbalance the cost of cellular MCA, as there is no evidence for MCA in whole-animal metabolism. Low rates of oxygen demand at low temperature are most likely related to a reduced ATP demand for protein turnover, ion pump activity and other aspects of basal metabolism (Clarke 1987). Especially protein turnover costs, which form a substantial fraction of resting metabolic costs (Hawkins et al. 1989; Wieser 1994), seem to be distinctly lower at low temperatures (Smith and Haschmeyer 1980; Clarke 1998). In the case of *A. colbecki*, increased protein stability leads to lower protein turnover (Storch and Pörtner 2003). Further savings are related to the downregulation of amount and flexibility of acid–base regulation (Pörtner 2002b).

Metabolism and growth

Our analysis of the relationship between ecological growth efficiency and temperature is based on a rather limited set of populations, where growth performance (P) and metabolic activity (SMR_{avg}) had been determined simultaneously. Nevertheless, the data point representing *A. colbecki* is very close to this regression line (Fig. 4), thus confirming that there are no detectable Antarctic effects on ecological growth efficiency in scallops.

Generally, the negative slope of the P/SMR_{avg}–to–temperature relation indicates that metabolic rates increase faster with temperature than does growth performance. The Q_{10} values computed from the corresponding Arrhenius models exemplify this difference: within the 0–28°C temperature range Q_{10} of scallop metabolic rate is 2.99 (Fig. 3a) and Q_{10} of scallop growth performance is 1.12 (Heilmayer, unpublished data). Metabolic Q_{10} is in the range of typical within-species Q_{10}-values reported in the literature (Bricelj and Shumway 1991), whereas growth performance Q_{10} is much lower. Studies of complex-integrated processes such as growth or respiration do not necessarily give useful information concerning cold adaptation. Growth, for example, may show compensation at the molecular level but still be slow for other reasons (for example, resource limitation). The complexity of such processes is emphasised by an empirical relationship obtained by Wieser (1994) and an experimental approach by Jørgensen (1988), suggesting that it costs about three times more metabolic energy to deposit one unit of body substance than it should cost on the basis of biochemical principles to synthesise this amount.

Conclusion

We could not detect any evidence for a whole-body MCA in *A. colbecki*, while existing cellular MCA seems to be counterbalanced by a combination of different adaptive mechanisms, mainly low protein stability costs at low temperature. Notwithstanding, the comparatively low standard metabolic rates of the Antarctic scallop appear to facilitate survival during the prolonged and strongly food-limited polar winter and do not enhance growth performance. Complete energy budgets at the individual and population level are required to decide whether or not the ecological efficiency of *A. colbecki* is in the range of non-Antarctic scallops. However, the P/SMR ratio is similar to temperate scallops.

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