

# Growth efficiency and temperature in scallops: a comparative analysis of species adapted to different temperatures

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## Summary

1. Data were collected on metabolic activity and growth in pectinid bivalves from published studies. The resulting database comprised three types of data sets: (i) synoptic data (13 populations, 7 species), where both individual growth performance and metabolism are known, (ii) 'metabolism only' data (82 populations, 13 species), and (iii) 'growth only' data (198 populations, 26 species).

2. In pectinid bivalves belonging to different species and living under different environmental conditions metabolic activity (standard metabolic rate, SMRAvg,  $Q_{10} = 2.97$ ) is more closely related to temperature than individual growth (overall growth performance, OGP index P,  $Q_{10} = 1.12$ ).

3. The synthesis of the two corresponding Arrhenius equations shows that the relationship between the SMRAvg-to-OGP ratio and temperature follows the Arrhenius model, too, with  $Q_{10} = 2.26$ .

4. SMRAvg-to-OGP is an inverse proxy for growth efficiency, hence growth efficiency decreases with rising temperature across a wide range of pectinid populations and species. Thus, there is strong empirical evidence that elevated temperature constrains growth efficiency in scallops and that adaptation does not fully compensate for this effect.

*Key-words:* Metabolic rates, overall growth performance, Pectinidae, temperature adaptation

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## Introduction

Temperature is one of the most significant abiotic factors in marine ecosystems. It affects almost all facets of organismal physiology, from the basic structures of macromolecules to the turnover rates of complex physiological systems. Hence, adaptation to environmental temperature has been recognized for a long time as one of the major challenges in evolutionary adaptation and is thought to be dependent, to a large extent, on the organism's ability to undergo metabolic reorganization on both short-term and evolutionary time-scales (Clarke 1998; Hochachka & Somero 2002; Pörtner 2002a,b). Metabolic rate is a measure of the energy consumed by all vital functions of an individual, including maintenance, growth and production of gametes. The impact of temperature on metabolic

energy turnover of ectothermic organisms, their short-term capability to respond to changing temperature and their long-term evolutionary adaptation to certain temperature regimes have been fairly well documented, although the underlying molecular and biochemical mechanisms remain to be fully elaborated (Clarke & Johnston 1999; Peck & Conway 2000; Pörtner 2002a,c; Heilmayer & Brey 2003). One key question is whether trade-offs are involved in such evolutionary compensation of temperature effects. For example, can we see changes in parameters such as growth efficiency across the natural range of temperature regimes from the polar cold to the tropical warmth?

Experimental, single-species studies of temperature adaptation indicate that growth efficiency (i.e. the quotient of production over assimilation; for review see Bayne & Newell 1983; Griffiths & Griffiths 1987) is negatively correlated with temperature. That is, elevated temperature constrains growth efficiency, and the short-term ability to adjust the individual energy budget to changing temperature is rather limited (e.g. Wieser *et al.* 1988; Present & Conover 1992; Clarke 2003). To identify evolutionary compensation we carried

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out a comparison of growth efficiency in taxonomically closely related species and populations across a wide temperature range at various latitudes.

There are, however, too few studies on growth efficiency across the ecological temperature spectrum (polar to tropical) to allow for a coherent analysis. Reliable data (i.e. growth, assimilation, respiration) require a costly and time-consuming input/output analysis for every single species or population. The few published studies focus either on intraspecific comparisons (e.g. Wieser *et al.* 1988; Present & Conover 1992; Beiras, Camacho & Albentosa 1994; Forsythe *et al.* 2002) or on age-related changes in single populations (e.g. Vahl 1981; MacDonald & Thompson 1986; Niu, Nakao & Goshima 1998; Urrutia *et al.* 1999), and do not allow for a general comparison on the species level across a wider temperature spectrum.

We tried to circumvent the missing data problem by constructing a versatile proxy for growth efficiency that can be computed from easy-to-measure parameters. Any comparative macro-scale study is a trade-off between the statistical power of large numbers of data and the introduction of taxon-related statistical noise. We tried to find a compromise by focusing our study on one single family, the Pectinidae, i.e. organisms with very similar body size, body shape, lifestyle and life-history features. Nonetheless, our proxy for growth efficiency may be examined from a reductionist's point of view. It does not aim to quantify growth efficiency precisely, but to establish an upper limit to the efficiency of conversion processes. We hope that our approach will encourage a fruitful discussion of evolutionary adaptations of growth efficiencies in the marine realm.

## Materials and methods

### LITERATURE DATA

The bivalve family Pectinidae consists of approximately 400 known living species. They cover a wide geographical and temperature range – from northern Norway (0–8 °C, e.g. *Chlamys islandica*) to the tropics (22–28 °C, e.g. *Euvola ziczac*) and further south to the Southern Ocean (–1.9 to +2 °C; *Adamussium colbecki*) (Brand 1991). In our data set many species are represented by several populations living separately at different temperatures. The genetic differentiation between populations is still under discussion and apparently contradictory (e.g. Beaumont 1982, 1991; Wilding, Beaumont & Latchford 1997; Wilding, Latchford & Beaumont 1998). Hence, under the assumption that gene flow between populations of a species is low, populations can be treated as separate entities (Garland, Harvey & Ives 1992; Foster & Cameron 1996), i.e. no statistical correction for combining different taxonomic levels is necessary. We obtained three types of data sets: (i) synoptic data (13 populations, 7 species), where both lifetime growth performance and metabolism of one population are known, (ii) ‘metab-

olism only’ data (82 populations, 13 species), and (iii) ‘growth only’ data (198 populations, 26 species).

### GROWTH PERFORMANCE

The three-parameter von Bertalanffy growth model (VBGF) is suitable to describe growth in pectinids as well as in other marine ectotherms.

$$M_t = M_\infty(1 - e^{-K(t-t_0)})^b, \quad \text{eqn 1}$$

where  $M_t$  is shell mass at time  $t$ ,  $M_\infty$  is the mean asymptotic mass,  $K$  is the Brody growth coefficient (which defines ‘speed’ of growth),  $t$  is the age,  $t_0$  is the theoretical age at which mass equals zero, and  $b$  equals the exponent of the exponential size–mass relation. The index of ‘overall growth performance’ OGP (for review see Brey 2001) is used to compare growth between populations or species. OGP is defined as the maximum growth rate (i.e. the growth rate at the inflexion point of the VBGF) calculated by

$$\text{OGP} = \log(KM_\infty). \quad \text{eqn 2}$$

### METABOLIC RATE

Respiration rates were used to approximate metabolic activity. Only data sets that met the following requirements were included in our analysis: (i) measurement of unfed, unstressed, inactive animals only (= resting or standard metabolism, as defined by Bayne & Newell 1983; Pörtner & Grieshaber 1993), (ii) temperature is within the natural range experienced by the species, and (iii) experimental animal size covers a sufficient size range of the population to allow a precise estimate of the scaling parameters within that species.

To remove the effect of body mass, the average specific metabolic rate ( $\text{SMR}_{\text{Avg}}$ ) of a standard-sized animal was computed according to Luxmoore (1984) by

$$\text{SMR}_{\text{Avg}} = aDM^{b-0.807}, \quad \text{eqn 3}$$

where  $a$  and  $b$  are constants of the corresponding relation between respiration rate and body mass of each population, and 0.807 is the mean pectinid-specific mass exponent calculated from 82 studies of 13 different species (for more details Heilmayer 2003). For ‘metabolism only’ data sets (no information on growth), DM is the geometric mean dry mass, whereas for synoptic data sets, DM is the dry mass at the inflexion point of the VBGF, i.e. the point that OGP refers to.

### WATER TEMPERATURE

Water temperature was either taken from the corresponding publication or inferred from the ‘World Ocean Database 2001’ of the National Oceanographic Data Centre ([http://www.nodc.noaa.gov/OC5/WOD01/pr\\_wod01.html](http://www.nodc.noaa.gov/OC5/WOD01/pr_wod01.html)), if necessary.

## STATISTICAL ANALYSIS

The Arrhenius model is likely to describe effects of temperature on whole-animal physiological processes best (Clarke & Johnston 1999); model parameters are estimated by linear regression of the linearized model.

Metabolic rate ( $SMR_{Avg}$ ):

$$\ln(SMR_{Avg}) = a_1 + b_1 \times 1/T \Leftrightarrow SMR_{Avg} = e^{a_1} e^{b_1/T} \quad \text{eqn 4}$$

Overall growth performance (OGP):

$$\ln(OGP) = a_2 + b_2 \times 1/T \Leftrightarrow OGP = e^{a_2} e^{b_2/T} \quad \text{eqn 5}$$

$T$  is the absolute temperature,  $a_1$  and  $a_2$  are the constants,  $b_1$  and  $b_2$  the slopes of the corresponding equations, i.e. Arrhenius activation energies.

The ratio of  $SMR_{Avg}$ -to-OGP is interpreted as an inverse proxy for growth efficiency, by reflecting the fraction of metabolic energy channelled into somatic growth. SMR includes the cost of growth on top of baseline metabolic costs. Once baseline costs or costs per unit of growth are high this may occur at the expense of lower growth performance. Regarding the synoptic data ( $N = 13$ ), population-specific  $SMR_{Avg}$ -to-OGP ratios were computed directly (data from Heilmayer & Brey 2003) and the relationship of  $SMR_{Avg}$ -to-OGP ratio to temperature was modelled by the corresponding Arrhenius equation. Regarding  $SMR_{Avg}$  values obtained from 'metabolism only' ( $N = 82$ ) data and OGP values obtained from 'growth only' data ( $N = 198$ ) a 'synthetic' model was obtained by mathematically combining equations 4 and 5:

$$\frac{SMR_{Avg}}{OGP} = \frac{e^{a_1} e^{b_1/T}}{e^{a_2} e^{b_2/T}} = e^{a_1 - a_2} e^{(b_1 - b_2)/T} \quad \text{eqn 6}$$

## Results

In scallops, standard metabolic rate ( $SMR_{Avg}$ ) is significantly related to temperature (Fig. 1):

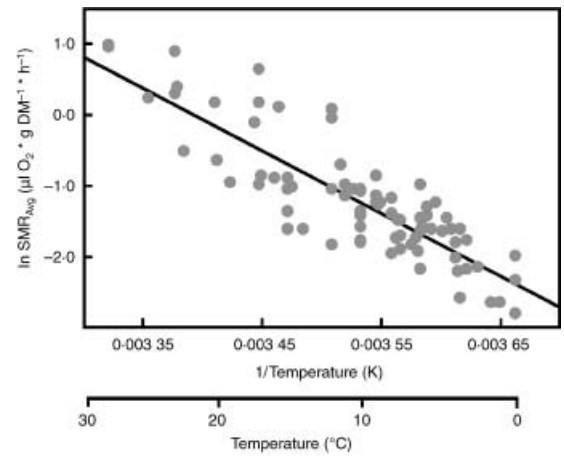
$$\ln(SMR_{Avg}) = 30.119 - 8876.41 \times 1/T,$$

( $N = 82$ , 13 species,  $r^2 = 0.724$ ,  $P < 0.001$ ). OGP is significantly related to temperature, too. The effect of temperature, however, is not as strong as in  $SMR_{Avg}$ , and the relationship is weaker (Fig. 2):

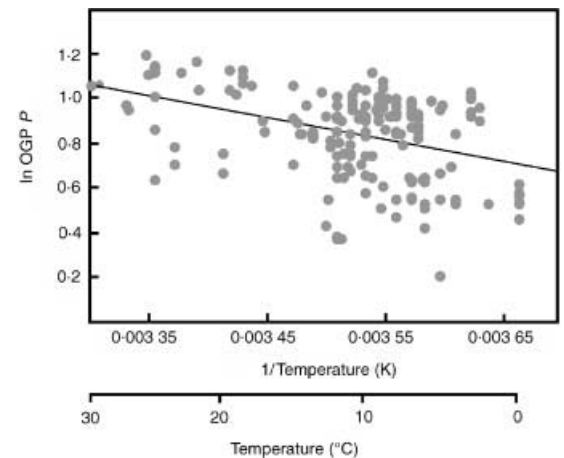
$$\ln(OGP) = 4.22 - 958.466 \times 1/T,$$

( $N = 198$ , 25 species,  $r^2 = 0.132$ ,  $P < 0.001$ ). The models are linear across the whole temperature range as indicated by the random distribution of residuals. Regarding the synoptically measured data, the inverse growth efficiency proxy  $SMR_{Avg}$ -to-OGP is related to temperature by:

$$\ln(SMR_{Avg}/OGP) = 21.265 - 6630.794 \times 1/T,$$



**Fig. 1.** Metabolic rates ( $\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) 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 given in Table A1 in the Appendix. Arrhenius plot, with fitted least-squares regression line:  $\ln(SMR_{Avg}) = 30.119 - 8876.41 \times 1/T$  (82 measurements, 13 species,  $r^2 = 0.725$ ) (modified after Heilmayer & Brey 2003).

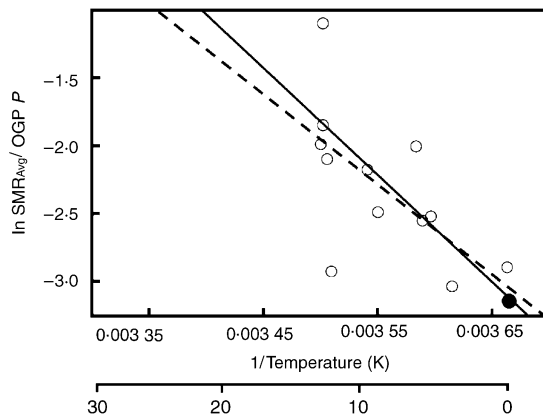


**Fig. 2.** Fitted Arrhenius model of the relationship between overall growth performance  $P$  and temperature for non-Antarctic and the Antarctic scallop:  $\ln(OGP P) = 4.22 - 958.466 \times 1/T$  (198 studies, 25 species,  $r^2 = 0.132$ ) (Authorities and references are taken from Heilmayer 2003).

( $N = 13$ , 7 species,  $r^2 = 0.479$ ,  $P < 0.001$ ). The parameter values of the 'synthetic' model are:

$$\ln(SMR_{Avg}/OGP) = 25.899 - 7917.944 \times 1/T.$$

Both models show essentially the same positive relationship between  $SMR_{Avg}$ -to-OGP and temperature, i.e. a negative relationship between growth efficiency and temperature (Fig. 3), indicating that animals achieve a higher growth performance relative to metabolic rate in the cold. Metabolic rates increase faster with temperature than growth performance, possibly as a consequence of enhanced maintenance cost or cost per unit growth or both. The temperature coefficients



**Fig. 3.** Relationship of the ratio between standard metabolic rate ( $SMR_{Avg}$ ) and overall growth performance (OGP) computed from the two appropriate Arrhenius equations according to equation 5. Regression line:  $\ln(SMR_{Avg}/OGP) = -25.899 + 7917.944 \times 1/T$ . Dashed line indicates the same relation in a synoptic data set where both parameters are known:  $\ln(SMR_{Avg}/OGP) = 21.265 - 6630.794 \times 1/T$  ( $N = 13$ , 7 species,  $r^2 = 0.479$ ,  $P < 0.001$ ). ●, *Adamussium colbecki*.

( $Q_{10}$ ) computed from the corresponding Arrhenius models exemplify this difference: within the 0–25 °C temperature range the  $Q_{10}$  of scallop metabolic rate is 2.97 (Fig. 1) whereas overall growth performance changes more slowly with temperature ( $Q_{10} = 1.12$ ) (Fig. 2). Arrhenius activation energies are 73.8 kJ mol<sup>-1</sup> K<sup>-1</sup> for  $SMR_{Avg}$  and 7.9 kJ mol<sup>-1</sup> K<sup>-1</sup> for OGP. The  $Q_{10}$  of the  $SMR_{Avg}$ -to-OGP-ratio derived from the above regression is 2.26 for the synoptic model and 2.65 for the synthetic model.

## Discussion

### IS THERE ANY EVIDENCE FOR THERMAL ADAPTATION?

Long-term changes in performance are caused either by acclimation or by adaptation. As the capacity for the thermal acclimation of performance is limited, an evolutionary adjustment is more likely (Bennett & Huey 1990). As indicated by the negative relationship with temperature, growth efficiency is far from being compensated for temperature effects. Our study even indicates a higher thermal sensitivity between species ( $Q_{10}$ : 2.65) than observed within individual species (range of  $Q_{10}$ : 1.11–1.66, median 1.35; Wieser *et al.* 1988; Present & Conover 1992; Beiras *et al.* 1994; Iguchi & Ikeda 1995; Forsythe *et al.* 2002; Niu *et al.* 2003).

The strong effect of temperature on growth efficiency indicates that growth efficiency is subject to physiological and/or thermodynamic constraints that are strongly coupled to temperature and that apparently cannot be overcome at reasonable costs. Theoretically there would be three ways to overcome these constraints: (i) an increase in assimilation efficiency, (ii) an increase in consumption and (iii) uncoupling of

metabolism from temperature. An increase in assimilation efficiency is unlikely, as the underlying physiological and enzymatic processes have been optimized during evolutionary history. Consumption is subject to strong ecological constraints by inter- and intraspecific competition for food. Moreover, optimum foraging theory demonstrates that each animal ‘design’ has an optimum consumption rate in relation to energy turnover (Wieser & Medgysey 1990; Jobling 1993). Metabolism can be uncoupled from ambient temperature only by complex and energetically expensive strategies such as behavioural avoidance or homeothermy (for review see Willmer, Johnston & Willmer 2002; Pörtner 2004). Both are unlikely to play a large role at all in hypometabolic aquatic ectotherms such as pectinids.

However, the study of species from thermally stable environments (i.e. deep sea, polar waters) is particularly useful for an understanding of the mechanisms of temperature compensation and their evolutionary significance in ectothermic animals. In particular, Antarctic species developed specific adaptations to their thermally stable environment over millions of years (Clarke 1998; Pörtner 2002a). Here more than anywhere else the explanation of a direct rate-limitation by temperature is intuitively appealing. Recent evidence demonstrates that the first line of thermal sensitivity becomes apparent at the highest functional level possible. Aerobic scope (i.e. the functional coordination of oxygen supply mechanisms to cover oxygen demand) limits energy availability and therefore probably growth, too (Guderley 1998; Pörtner 2001, 2002a,b). As shown in various studies (for review see Pörtner 2001; Pörtner *et al.* 2001; Hochachka & Somero 2002; Pörtner 2002a,b), shortage of organismic aerobic capacity in the cold is compensated for at the cellular level by mitochondrial proliferation and associated molecular and membrane adjustments: (i) low mitochondrial aerobic capacities and H<sup>+</sup> leakage rates (Johnston *et al.* 1998; Pörtner, Hardewig & Peck 1999; Hardewig *et al.* 1999); (ii) changes in the kinetic characteristics of mitochondria and enzymes reflect differences in metabolic regulation and are inevitably involved in adaptation and acclimation to ambient temperature (Torres & Somero 1988; Crockett & Sidell 1990; Somero 1995; Kawall *et al.* 2002; Sukhotin & Pörtner 2001); (iii) elevated Arrhenius activation energies of mitochondrial proton leakage and of enzymes (i.e. high kinetic barriers to metabolic flux; Pörtner *et al.* 1999; Hardewig *et al.* 1999); and (iv) down-regulation of the rate and flexibility of acid–base regulation (Pörtner 2002b). The pattern observed among the pectinids indicates that these metabolic adjustments effect a reduction of baseline metabolic costs in the cold, correspondingly a larger fraction of available energy is allocated to growth and growth efficiency increases.

According to the macro-scale pattern discussed here it appears relevant to consider that temperature-dependent trade-offs may differ between short-term

and long-term adjustments, i.e. cold-acclimated and cold-adapted animals (for review see Pörtner 2001; Pörtner *et al.* 2001). Recently Pörtner *et al.* (2001) provided evidence for an inverse relationship between growth performance and standard metabolic rate in one fish species (*Gadus morhua*), i.e. temperature-specific growth was lower at higher SMR in Arctic than in temperate populations. Such a difference between stenotherms and eurytherms is not evident from the data available for pectinids, possibly because of insufficient data from cold, unstable climates. Nonetheless, trade-offs between growth performance and metabolic rate apparent in macro-scale comparisons suggest that low SMRs reflect reduced cost of maintenance and support allocation of a larger fraction of metabolic energy to growth (Bayne & Newell 1983; Hawkins *et al.* 1998; Pörtner 2002c). Thus they support enhanced levels of growth performance and efficiency at lower temperatures.

We must conclude that maximizing individual growth efficiency is not a primary selection criterion in evolution (see also Calow 1983; Present & Conover 1992). Obviously, the actual individual growth efficiency results from complex temperature-dependent trade-offs within the overall energy budget of the organism. Hence evolutionary development may rather proceed towards an 'optimum' growth efficiency specific for the temperature regime at which the organism lives. The strong empirical relationship between growth efficiency and temperature found in scallops is in line with this idea.

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## Appendix

Table A1.

<i>Adamussium colbecki</i>	Heilmayer & Brey (2003)
<i>Aequipecten opercularis</i>	Vahl (1972); McLusky (1973); Heilmayer <i>et al.</i> (2004)
<i>Argopecten circularis</i>	Silva Loera (1986)
<i>Argopecten irradians concentricus</i>	Kirby-Smith (1972); Barber & Blake (1985); Yang <i>et al.</i> (1998a); Lu, Blake & Torres (1999)
<i>Argopecten irradians irradians</i>	Bricelj, Epp & Malouf (1987)
<i>Chlamys deliculata</i>	Mackay & Shumway (1980)
<i>Chlamys hastate</i>	Bernard & Noakes (1990)
<i>Chlamys farreri</i>	Yang <i>et al.</i> (1998b)
<i>Chlamys islandica</i>	Vahl (1978); Vahl & Sundet (1985); Schmid (1996)
<i>Mimachlamys varia</i>	Shafee (1982)
<i>Mizuhopecten yessoensis</i>	Fuji & Hashizumu (1974)
<i>Placopecten magellanicus</i>	MacDonald & Thompson (1986); Shumway, Barter & Stahlnecker (1988); Grant & Cranford (1991); Pilditch & Grant (1999)
<i>Zygochlamys patagonica</i>	Heilmayer <i>et al.</i> (2001)

Table A2.

<i>Aequipecten opercularis</i>	Vahl (1972); McLusky (1973); Heilmayer <i>et al.</i> (2004)
<i>Chlamys islandica</i>	Vahl (1978); Vahl & Sundet (1985)
<i>Mimachlamys varia</i>	Shafee (1982)
<i>Mizuhopecten yessoensis</i>	Fuji & Hashizumu (1974)
<i>Placopecten magellanicus</i>	MacDonald & Thompson (1986); Shumway, Barter & Stahlnecker (1988)
<i>Zygochlamys patagonica</i>	Heilmayer <i>et al.</i> (2001)
<i>Adamussium colbecki</i>	Heilmayer <i>et al.</i> (2003)