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Temperature effects on summer growth rates in the Antarctic scallop, *Adamussium colbecki*

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Abstract Annual growth rates of Antarctic marine organisms are low compared to their relatives from warmer waters. Previous studies hypothesise that high food availability during austral spring–summer may enable Antarctic invertebrates to attain comparatively high short-term growth rates despite the low temperature. Neither a temperature-growth experiment with juvenile *Adamussium colbecki* (Smith 1902) nor the comparison of *A. colbecki* summer growth rates with an empirical scallop specific growth-to-temperature relationship could confirm this hypothesis. Hence, summer growth rates of young, immature *A. colbecki* are strongly affected by temperature, i.e. no "uncoupling" from temperature.

Keywords *Adamussium colbecki* · Antarctic scallop · Growth · Growth rate · Temperature

Introduction

Antarctic marine metazoans are characterised by low overall metabolic rates, low levels of activity, low turnover ratios and slow individual growth (Brey and Clarke 1993; Arntz et al. 1994). Historically this has been explained as an unavoidable consequence of lowered temperature on the physiology of these organisms. More recently it has been proposed that seasonal resource limitation rather than temperature represents the restricting factor for polar marine environments (Arntz et al. 1994; Clarke 1998). In Polar regions, productivity and consequently growth is usually confined to the short summer season (e.g. Nolan and Clarke 1993; Barnes 1995). There is some evidence that during periods of high food supply (spring–summer) growth rates of Antarctic invertebrates may be as high as in their temperate relatives (e.g. Clarke 1988; Brey and Hain 1992; Ahn et al. 2003). Evidence for the role of seasonality comes from bivalves, where latitudinal variation in annual shell growth rate is strongly correlated with the number of days in the year on which feeding was possible (e.g. Chauvaud and Strand 1999), as well as from the Antarctic invertebrates, such as the bryozoan *Cellarinella* (Barnes 1995) and the sea urchin *Sterechinus neumayeri* (Brockington et al. 2001).

Evidence suggests that the capacity for growth (i.e. maximum growth potential) within taxonomically closely related species may vary inversely with the length of the growing season across a latitudinal gradient either to compensate in part (Levinton and Monahan 1983) or even in full (MacDonald and Thompson 1988) for environmental effects (countergradient variation, e.g. Conover and Schultz 1995; Arendt 1997). However, most growth comparisons across latitudes are based largely on the comparison of annual rates. Hence, it may be important to measure growth rates on time scales that are appropriate to the individual in nature (i.e. by explicitly comparing maximum growth rates). Thus, the short growing season may constrain individual growth more than the permanently low temperature (Clarke 1998; Peck 2002). Our study investigates whether this general pattern may be true for the Antarctic scallop, *Adamussium colbecki* (Smith 1902), a key species in Antarctic shallow-water communities (Cattaneo-Vietti et al. 1997;

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Chiantore et al. 2000). Based on a comparison of our own and published experimental data, we ask two questions: (1) Is the growth rate-to-temperature relationship of *A. colbecki* in a 'normal' range compared to lower latitude scallop species and (2) is the summer growth rate of *A. colbecki* above the temperature-to-growth rate range found in temperate and warm water scallops?

Material and methods

Adamussium colbecki summer growth experiment

In summer 1999/2000, 28 juvenile *A. colbecki* [size range: 10.2–16.9 mm shell height: 4.7–33.9 mg shell free dry mass (SFDM)] were collected near the Italian Antarctic station 'Terra Nova Bay' (74°41.9'S, 164°07.5'E) from 60 m to 80 m water depth. Animals were incubated for 12 h in slightly aerated filtered seawater with calcein (2,4-bis-[N,N'-di(carbomethyl)-aminomethyl]-fluorescein: Sigma C0875) (1 g calcein l^{-1}, pH 8; modified after Dahm 1996). Calcein was used for setting artificial growth marks in calcium carbonate skeletons as it is incorporated into the growing calcium carbonate structure and fluorescences under UV light. It has been used previously in various taxa, including fishes (e.g. Mohler 1997), echinoderms (e.g. Dahm 1996) and molluscs (e.g. Kaehler and McQuaid 1999; Moran 2000; Clarke et al. 2004). After incubation, animals were randomly divided into three groups maintained under natural light and food regime: (1) Group A1 ($N=10$) and Group A2 ($N=12$) at actual environmental temperature (0 ± 0.5° C) for a period of one, respectively, two weeks, and (2) Group B ($N=6$) for one week at 3 ± 0.5°C. Total growth increment (calcein mark to shell edge) was measured under UV light with a Wild Microscope M6, equipped with a microscale and transformed to daily shell growth rate.

Empirical data on scallop growth

A general relation between temperature and short-term growth rates in scallops was based on growth data from the literature, which (1) referred to juvenile, premature individuals and (2) were measured during the main growth period of the species.

Hypothesis testing

(a) Is temperature sensitivity of the summer shell growth rate of *A. colbecki* in the 'normal' range observed in lower latitude scallops?

If growth of *A. colbecki* is less temperature sensitive, than an additional increase in temperature on top of enhanced food availability, should cause a comparatively low increase in growth rate. To test whether a temperature increase of 3°C increased the summer growth rate of juvenile *A. colbecki* less (H_0) or as strongly as (or stronger than) (H_A) predicted by the overall empirical relation between temperature and growth rate in pectinids, we compared the Q_{10} values of *A. colbecki* growth with corresponding Q_{10} values from published comparable intraspecific growth studies.

(b) Is the summer growth rate of *A. colbecki* above the temperature-to-growth rate range found in temperate and warm water scallops?

If summer growth rates of *A. colbecki* are "less" limited by temperature, than they should substantially deviate from the temperature-to-growth rate range found in scallops living in temperate and warm waters. This would indicate specific temperature adaptations in the Antarctic scallop. An ANCOVA (growth rate as dependent variable, Antarctic ↔ non-Antarctic as factor and 1/T as a covariate) was applied to our collection of scallop growth data to test whether summer growth rates of *A. colbecki* are within the range (H_0) or higher (H_A) than predicted from the relation between temperature and (summer) growth rates.

Results and discussion

Adamussium colbecki summer growth rates

Individual daily growth rates in calcein marked *A. colbecki* ranged from 10.7 μm/day to 84 μm/day (Fig. 1). Mean daily shell growth rates at 0°C, 19.75 ± 6.26 μm/day in Group A1 and 19.28 ± 8.10 μm/day in Group A2, were indiscriminable but were significantly ($\alpha = 0.05$) lower than growth rates at 3°C, 71.25 ± 14.14 μm/day in Group B (one-way ANOVA with Student-Newman post hoc test). Daily summer growth rates of *A. colbecki* are clearly higher than published data for other Antarctic bivalves (e.g. *Yoldia eightsi*, Peck et al. 2000), emphasizing that *A. colbecki* is a fast growing species

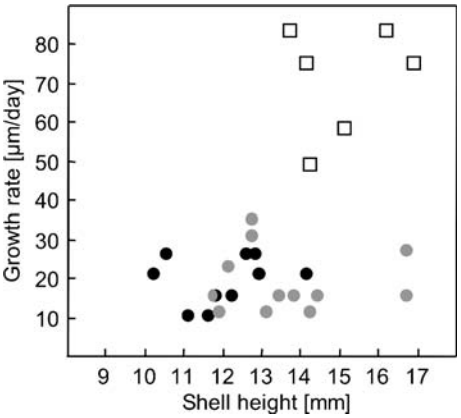

Fig. 1 *Adamussium colbecki*. Relationship between shell height and daily growth rate within juvenile Antarctic scallops maintained at two different temperatures. Growth estimates were obtained by increment determination after one, respectively, two weeks (*circles*: Group A1, 0°C, one week; *dots*: Group A2, 0°C, two weeks; *squares*: Group B, 3°C, one week)

(Heilmayer et al. 2003). Growth rates at 0°C are in the range of data for adult individuals from Mc Murdo Sound (Berkman 1990). Hence, in contrast to annual growth rates (Heilmayer et al. 2003), there is no evidence for age dependence in short-term growth rate as observed for other mollusc species (i.e. Sukhotin et al. 2002). This may be due to (1) different environmental conditions of both study sites or (2) a compensatory growth increase after a period of inhibition as observed frequently in marine poikilotherms (e.g. Schultz et al. 2002).

Temperature sensitivity of *A. colbecki* summer growth rates

The threefold increase from 0°C to 3°C corresponds to a Q_{10} value of 71.28, which is clearly the highest Q_{10} value found among temperate and warm water scallops, which range from 2.68 (overall comparison, Fig. 2) to 3.19 (*Placopecten magellanicus*). These findings indicate that summer growth rates of *A. colbecki* are not less temperature sensitive than in other pectinids. On the contrary, the high Q_{10} values at low temperatures may be indicative of a change in the properties of the underlying biochemical systems, such that the energy barriers to the process questioned are increased (Clarke 1988, 2003). High Q_{10} values (i.e. being above physiological normal values) have been reported for various complex processes of Antarctic invertebrates, such as growth (Clarke 1988) or embryonal development time (Yoshida et al. 2004). The mechanism, however, underlying the high increase of Q_{10} values is still subject of ongoing discussions.

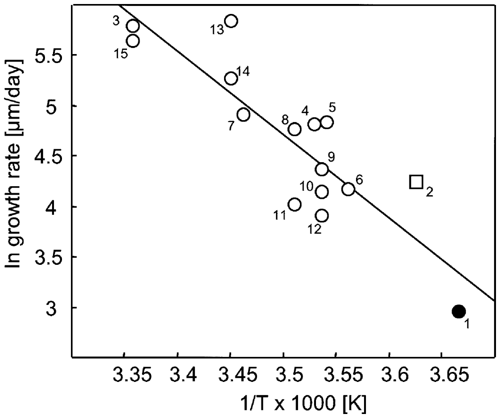

Fig. 2 Mean daily shell growth (µm/day) for six scallop species from different latitudes. Shown are values measured at main growth periods in juvenile/premature scallops: *1–2*: *Adamussium colbecki* (*1* this study 0°C, *2* this study, +3°C); *3*: *Argopecten circularis* (Ruiz-Verdugo and Cáceres-Martinez 1991); *4–5*: Chlamys *islandica*(Thorarinsdôttir 1994); *6*: *Mizuhcopecten* yessoensis (Maru 1985); *7–12*: *Placopecten magllanicus* (Dadswell 1989; Chandler et al. 1989; Dadswell and Parsons 1991; Thouzeau et al. 1991; Parsons et al. 1993); *13–14*: Pecten *maximus* (Chauvaud et al. 1998; *13* 1-year-old, *14* 2-years-old); *15*: Pecten vogdesi (Ruiz-Verdugo and Cáceres-Martinez 1991). Arrhenius plot, with fitted least-squares regression line (only populations 3 to 15): ln shell growth (µm/day) = 33.65–8.268 1,000/T ($N=13$, $r^2=0.693$, $P<0.001$)

Specific temperature adaptations in *A. colbecki*

Daily growth rates of scallops are significantly and positively related to temperature (Fig. 2), as indicated by the Arrhenius equation: ln shell growth (µm/day) = 33.65−8.268 1,000/T ($N=13$, $r^2=0.693$, $P<0.001$). There is no significant regional effect on growth rate detectable (ANCOVA: growth rate as dependent variable, Antarctic ↔ non-Antarctic as factor and $1/T$ as a covariate) ($F=0.0061$, $P>0.5$). Thus, growth rates of *A. colbecki* do not differ from growth rates of other scallop species if the overall temperature dependence has been accounted for. Our results confirm previous results based on a latitudinal comparison of annual rates (e.g. Harrington 1987; Heilmayer et al. 2003, 2004). In contrast, an increased growth rate working against the limiting effects of cold temperature are widespread in fishes (Conover and Schultz 1995) and marine invertebrates, including copepods (Lonsdale and Levinton 1985), polychaetes (Levinton and Monahan 1983) and gastropods (Parsons 1997) (countergradient growth).

The observed growth pattern of Antarctic scallops raises a number of issues concerning trade-offs between the capacity for growth and other physiological or life-history traits. Antarctic herbivores may employed a variety of feeding and growth strategies to cope with extreme food and environmental seasonality: (1) efficient feeding, feeding throughout the whole year (Barnes 1995; Peck et al. 2000) (2) and brief period of intensive feeding and growth during austral summer followed by winter starvation (Clarke 1988; Barnes 1995). Further field studies, especially under winter conditions, are necessary to determine the factors underlying the growth patterns in *A. colbecki*.

Conclusions

Growth rates of *A. colbecki* are neither less temperature sensitive, than in temperate and warm water pectinids, nor do they deviate from the growth rate-to-temperature relation common to all scallop species (no evidence for countergradient variation). There are no unique growth characteristics of Antarctic scallops, once the effects of temperature have been eliminated (i.e. no "uncoupling" from temperature). Thus, our observations indicate that temperature is a major constraint of summer growth rates in *A. colbecki* .

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Appendix

Table a Short-term growths rates in different scallops, which refer to juvenile, premature individuals and are measured during the main growth period of the species

Pop No.	Temp [°C]	Growth [μm/d]	Experimental conditions/ Growth measurements	Reference
Adamussium colbecki				
1	0	19.81	Laboratory study with natural food; instantaneous growth rates; individuals marked with calcein	This study
2	3	71.25		This study
Argopecten circularis				
3	25	337	Field study; analysis of SID	Ruiz-Verdugo and Cáceres-Martinez 1991
Chlamys islandica				
4	9.6	130	Field study (1st year); analysis of SID; monthly growth measurements	Thorarinsdôttir 1994
5	10.5	126	Field study (2nd year); analysis of SID; monthly growth measurements	Thorarinsdôttir 1994
Mizuhopecten yessoensis				
6	8	66	Field study; analysis of SAD	Maru 1985
Placopecten magellanicus				
7	10	65	Field study; instantaneous growth rates; monthly growth measurements	Dadswell 1989
8	12	120	Field study; 1st year of growth; instantaneous growth rates; bi-monthly growth measurements	Dadswell & Parsons 1991
9	16	140	Field study; 1st year of growth; instantaneous growth rates; bi-monthly growth measurements	Dadswell & Parsons 1991
10	10	81	Field study; analysis of SAD	Chandler et al. 1998
11	10	51	Field study; analysis of SAD	Thouzeau et al. 1991
12	12	57	Field study; analysis of SID; image analysis of individuals marked with Alizarin red S dye	Parsons et al. 1993
Pecten maximus				
13	17	200	first -year-old; image analysis of daily growth rings	Chauvaud et al. 1998
14	17	350	two-years-old; image analysis of daily growth rings	Chauvaud et al. 1998
Pecten vogdesi				
15	25	289	Field study; analysis of SID	Ruiz-Verdugo and Cáceres-Martinez 1991

Study conditions are summarized as far as available
SID Size-increment-data; *SAD* Size-at-age data

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