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Phenotypic plasticity of body size at different temperatures in a planktonic rotifer: mechanisms and adaptive significance

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Summary

1. Larger body size at low temperatures is a commonly observed phenomenon in ectothermic organisms. The mechanisms that lead to this pattern and its possible adaptive significance were studied in laboratory experiments using the parthenogenetically reproducing rotifer *Synchaeta pectinata*.

2. At low temperatures of 4 °C mean body volume was 46% larger than in individuals cultured at 12 °C. Egg volume was 35% larger in low *vs* high temperatures.

3. Larger body size at low temperatures was caused by two mechanisms. First, when exposed to low temperatures, mothers laid larger eggs and the hatchlings of these eggs developed into larger adults (irrespective of temperature). Second, individuals cultured at low temperatures grew to a larger body size during their juvenile phase. The former mechanism had a greater influence on adult size than the latter.

4. The production of larger eggs at low temperatures seemed to be due to a higher reproductive investment into individual offspring as it occurred independently of differences in maternal size.

5. Life table experiments showed that offspring from small eggs (produced at high temperatures) had a significantly higher population growth rate than offspring from large eggs, when cultured at high temperatures. This was mainly due to an increase in fertility during the first days of adult life.

Key-words: Bergmann's rule, egg size, life table, *Synchaeta pectinata*, zooplankton

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Introduction

In both aquatic and terrestrial habitats, animals usually attain a larger adult body size when growing at low temperatures. For endothermic organisms this phenomenon became known as 'Bergmann's rule' (Bergmann 1847). Bergmann's original, and still widely accepted, adaptive explanation states that a large body size confers an energetic advantage by reducing heat loss at low temperatures. This explanation is clearly inappropriate for ectothermic organisms, yet more than 80% of animals with this lifestyle show the same pattern in body size (Atkinson 1994). The lack of explanations for Bergmann's rule in ectotherms has stimulated a lot of research and discussions in recent years (Berrigan & Charnov 1994) (for a summary, see Atkinson & Sibly 1997). There is still controversy about whether a large body size at low temperatures is adaptive at all, or if it is just the unavoidable consequence of physiological constraints (Van Voorhies 1996; Partridge & Coyne 1997; Van Voorhies 1997).

Large body size at low temperatures can be the result of an evolutionary response to temperature, a developmental response, or a combination of these two processes. The evolutionary response results from differences among genotypes owing to selection over several generations, i.e. genotypes that confer a large body size become more abundant in populations living in cold environments. Indirect evidence for this response has been provided by 'common garden experiments', in which individuals of populations from different latitudes or altitudes are reared under identical conditions in the laboratory (e.g. Berven 1982; Lonsdale & Levinton 1985). Studies on artificial selection using *Drosophila* as a model have provided direct evidence for the evolutionary response to temperature (Partridge *et al*. 1994). The developmental response to temperature is a form of phenotypic plasticity. One genotype (or closely related individuals) may grow to different adult body sizes depending on the temperature of its environment. Evidence for this response has been

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provided by a large number of studies (summarized in Atkinson 1994). Both the evolutionary and developmental response generally result in a larger body size at low temperatures. This similarity suggests that both responses may have the same underlying principle (Partridge & French 1996).

At least two mechanisms can account for the developmental response of body size to temperature. First, allocation to body growth during the juvenile phase may be different in low *vs* high temperature environments. At low temperatures individuals may allocate more material to body growth and therefore mature at a larger size (Atkinson 1994). Second, adult body size may depend on the size at birth, i.e. it may be determined by what the previous generation allocated to each individual offspring. Large offspring at low temperatures has been observed frequently (Atkinson *et al*. 2001). Moreover, size at birth can strongly influence adult body size, for it has been shown that larger eggs/offspring will develop into larger adults (e.g. Lampert 1993). In the following, I will use the terms 'direct effect of temperature' for the effect of temperature on body size via juvenile growth and 'maternal (maternally transmitted) effect of temperature' for the effect of temperature on body size via offspring size adjustments of the mother. In practice, it is difficult to distinguish between the direct and the maternal effect of temperature, because in sexually reproducing organisms genetic variation can confound these patterns of phenotypic plasticity (but see Crill, Huey & Gilchrist 1996). Therefore clonally reproducing organisms are a better choice when studying such questions.

One aim of this paper is to evaluate the contributions of the direct effect *vs* the maternal effect of temperature on adult body size, using the planktonic rotifer *Synchaeta pectinata* as a model organism. As rotifers reproduce by parthenogenesis, maternal effects can be studied in a very straightforward way. To measure maternal effects, one would rear mothers of one clone under various environmental conditions and measure traits of interest in their parthenogenetically produced offspring under identical environmental conditions. Any systematic differences among the offspring produced in this way must be due to the environmental factors acting on the maternal phenotype. In terms of their life histories, rotifers are similar to other iteroparous organisms and may therefore serve as general models. However, their generation times are much shorter (several hours to a few days), which facilitates experimental studies even when conducted at low temperatures. There have been some experimental studies that showed body size in rotifers increases at low temperatures (summarized in Atkinson 1994). Field observations at different times (i.e. temperatures) of the year are consistent with this result because they show negative correlations between body size and water temperature (e.g. Green 1998).

In this paper I examined how both processes – the maternal effect and the direct effect of temperature – contribute to determination of body size. In laboratory experiments with the planktonic rotifer *Synchaeta pectinata* I tested the following hypotheses:

1. Adult body size increases at low temperatures because the previous generation produced larger offspring (maternal effect of temperature).
2. Adult body size increases at low temperatures because individuals grow to a larger size during their juvenile phase (direct effect of temperature).

These hypotheses are not mutually exclusive – both processes may contribute to body size or interact synergistically.

One result of this study was that *Synchaeta* produced larger offspring at low temperatures. Therefore, I additionally tested the hypothesis that this plasticity in offspring size might be adaptive, i.e. that large offspring have an advantage (a higher population growth rate) at low temperatures.

Materials and methods

CULTURE CONDITIONS AND GENERAL PROCEDURES

All rotifers used in the experiments were parthenogenetically produced offspring of one individual *S. pectinata* that was isolated from Schöhsee, a mesoeutrophic lake in Northern Germany. *Synchaeta* were cultured in artificial ADaM medium (Klüttgen *et al*. 1994), which was supplemented with 10% MBL (Marine Biological Laboratory) medium (Guillard 1975) and 2·2 mg l^{-1} Na_2EDTA (ethylenediaminetetraacetic acid) to improve the growth conditions for the food alga *Cryptomonas erosa* var. reflexa (kindly supplied by J. J. Gilbert). Stock cultures were maintained in temperature-controlled cabinets at 4, 8 and 12 °C and food concentrations were kept constantly high (~2–3 mg °C l^{-1}). During the experiments *S. pectinata* were cultured individually in 12-well tissue culture plates, each well containing 3 ml food suspension. For more details on the culture method see Stelzer (2001).

The food alga *Cryptomonas* was grown in MBL medium in semicontinuous culture, at continuous illumination (100 µmol quanta m^{-2} s^{-1}), and a temperature of 15 °C. Under these culture conditions the carbon content of one *Cryptomonas* cell was 219 pg per cell (Stelzer 1998). Alga concentrations were measured with an electronic particle counter (CASY, Schärfe System, Reutlingen, Germany) and diluted with ADaM and MBL medium to yield the desired food concentration and chemical composition of the rotifer culture medium.

Measurements of body size were done with an image analysis system (SIS, Münster, Germany), connected to an inverted microscope. In most experiments, living animals were measured in a plankton compression chamber according to Uhlig (Hydrobios, Kiel, Germany).

With this chamber it is possible to slow down the swimming speed of *Synchaeta*, which facilitates measurements on body size (Stelzer 2001). Body volume was calculated from measurements of body length and breadth according to the formula suggested by Ruttner-Kolisko (1977). In the first experiment (see below), animals had to be fixed with Lugol's solution before the measurements for logistic reasons. As *Synchaeta* contracts its body under such a treatment, the formula of Ruttner-Kolisko (1977) was inappropriate and body volume was therefore calculated assuming the shape of an ellipsoid of rotation. Sizes of the spherical eggs were calculated from measurements of egg diameters.

EXPERIMENTS

All experiments were conducted at temperatures of 4, 8 or 12 °C. These temperatures are well within the range at which *Synchaeta pectinata* is most abundant in the field (Berzins & Pejler 1989). In Schöhsee, the lake where the experimental clone originated, *S. pectinata* achieves maximum population densities in early spring (Fußmann 1996). Both in the laboratory and in the field, *Synchaeta* follows the temperature-size rule, and displays larger body size at low temperatures and smaller size at high temperatures (C. P. Stelzer personal observation). In the *Results* section, I will show some size measurements from laboratory cultures that support this observation.

To assess phenotypic plasticity of body size and egg size along a temperature gradient, stock cultures of *S. pectinata* were kept at 4, 8 and 12 °C, respectively. Regular inspections were made to keep animal densities at 1–3 ind. ml^{-1} and the food concentrations at 2–3 mg C l^{-1}. If necessary, stock cultures were diluted with fresh culture medium or fed with a concentrated *Cryptomonas* suspension. After the animals had acclimated for at least 4 weeks, random samples were taken from each culture and fixed with four drops of Lugol's solution per 100 ml. At all three temperatures body size (n = 42–128) and egg size (n = 37–52) were measured. As it was not possible to discriminate between juvenile and adult *S. pectinata* in samples fixed with Lugol's solution, body sizes of all age classes were pooled. This increased the variance in the body size but prevented subjectivity due to non-random sampling of different age classes across the treatments.

One experiment was conducted to assess the direct effect of temperature on somatic growth and on egg size in *Synchaeta*. Six eggs, laid by females cultured at 8 °C and not older than 6 h, were incubated individually at 4 °C or 12 °C. Offspring that hatched from these eggs were cultured at 3 mg C l^{-1} until they were adults and had laid their fourth egg. Body size was measured at regular intervals (24 h in the 4 °C animals, 12 h in the 12 °C animals). As the animals became adults, their eggs were collected in the order in which they were laid and egg size was measured.

Another experiment was conducted to assess the maternal effect of temperature, by determining how the rearing temperature of the mother affects somatic growth and egg size in their daughters. The experimental design was similar to the previous experiment, except that this time the eggs were isolated from females cultured at 4 °C and 12 °C, respectively, and subsequently incubated at 8 °C. The eggs in this experiment were not older than 12 h (4 °C) and 3 h (12 °C) in order to account for the different times of embryonic development. This guaranteed that at the start of the experiment all animals were at the same stage of development (embryonic development lasts for 1 day at 12 °C and 4 days at 4 °C; C. P. Stelzer personal observation). Body size was measured in 12-h intervals, eggs were collected and their size was measured.

One result of the experiments described above was that *Synchaeta* produced large eggs when they were cultured at low temperatures. To test whether this was an adaptive response, I determined the population growth rate of large *vs* small offspring at high (12 °C) and low (4 °C) temperatures using life table response experiments. If a large egg size would be adaptive to low temperatures, offspring of larger eggs should have a higher population growth rate at low temperatures (and the same for small eggs at high temperatures).

Differences in egg size were induced by culturing their mothers at 4 °C (large eggs) or 12 °C (small eggs). Large eggs were not older than 12 h and small eggs not older than 3 h when they were exposed to one of the four experimental conditions: 4 °C at high food concentrations (3 mg C l^{-1}), 4 °C at low food concentrations (0·3 mg C l^{-1}), 12 °C at high food concentrations and 12 °C at low food concentrations. In total, the experiment consisted of eight life tables (all combinations among two egg sizes, two temperatures and two food concentrations).

During the experiments individuals were transferred daily into new food suspensions until they died. Eggs were counted and removed each day. Unfortunately, the food alga cultures crashed on the 25th day of the experiment for unknown reasons. At this time most of the 4 °C animals were still alive, so their life tables were incomplete. Of those, the ones that were cultured at the high food concentration (3 mg C l^{-1}) had laid on average their 13th egg by then. As comparisons were drawn between large and small eggs separately for each treatment, this event did not affect the subsequent analysis. However, the absolute values of the population growth rates in all 4 °C treatments might have been underestimated.

Population growth rates and their confidence intervals were calculated from Leslie matrices, which were derived from the life tables using the approximations for a 'birth flow population' (Caswell 1989). Confidence intervals were estimated using a jack-knife resampling method described in Caswell (1989). Differences between the growth rates of large *vs* small eggs were considered statistically significant if the 95%

confidence interval of one group did not overlap with the population growth rate of the other group. In those cases where significant differences were found, a sensitivity analysis (Caswell 1989) was performed subsequently. This analysis allowed me to identify the vital rates (survival or fecundity at different age classes) that contributed most to the observed differences in the population growth rate. All calculations were done using the interactive programming language MATLAB (Matworks Inc., Natick, MA, USA).

Results

To confirm that the widespread relationship between body size and temperature does also apply for the rotifer *S. pectinata*, the size of individuals from laboratory cultures at different temperatures was measured. Body size and egg size were significantly larger in animals that had been cultured at low temperatures (egg size: ANOVA, $P < 0{\cdot}001$; body size: Kruskal–Wallis test, $P < 0{\cdot}05$). Mean body volume was 46% larger in 4 °C cultures *vs* 12 °C cultures and mean egg volume was 35% larger (Fig. 1). There was much variation in body size, probably due to the inclusion of juveniles, and the distribution of body sizes was skewed towards smaller size classes (Fig. 1a). However, it is obvious that the upper limit of body size consistently increased at low temperatures.

To investigate how differences in adult size can arise,

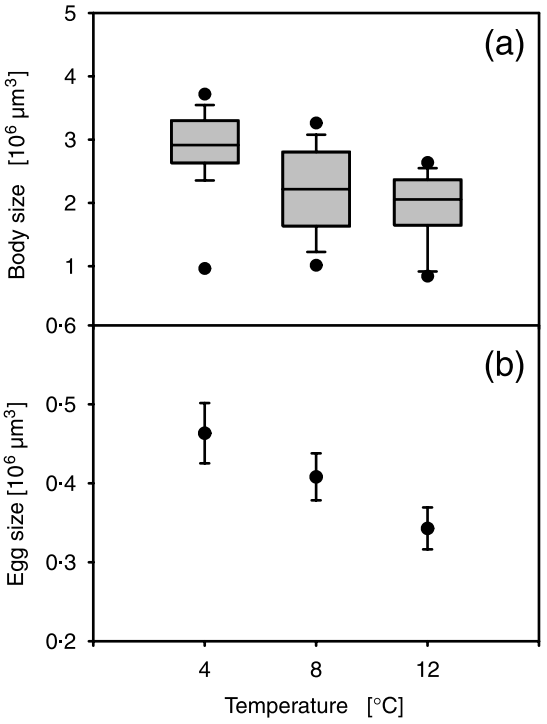

Fig. 1. Phenotypic plasticity of *Synchaeta pectinata*. Box plots (median, 10th, 25th, 75th and 90th percentiles; dots are 5th/95th percentiles) of body size (a) and means ± standard deviations of egg size (b) at different temperatures are shown. Sample sizes were $n = 42$–128 for body size and $n = 37$–52 for egg size measurements.

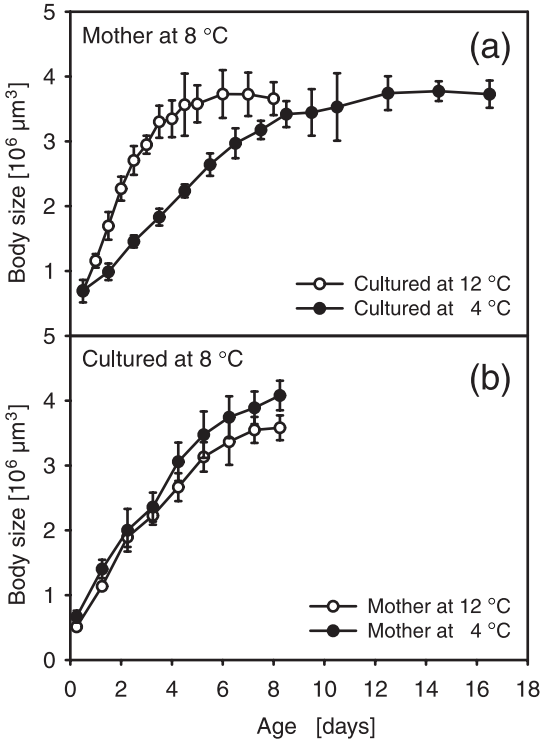

Fig. 2. Somatic growth of *Synchaeta pectinata* during the juvenile and early adult phase at different temperatures. (a) Direct effect of temperature, showing growth offspring of mothers cultured at 8 °C and subsequently cultured at 4 °C or 12 °C. (b) Maternal effect of temperature, showing growth of animals cultured at the same temperature (8 °C) but originating from mothers cultured at 4 °C or 12 °C . Figure shows means and standard deviations ($n = 6$).

growth curves were established for individuals that were grown at different temperatures (Fig. 2a) and individuals, whose mothers were grown at different temperatures (Fig. 2b). When cultured at 12 °C *Synchaeta* grew faster and reached maturity earlier (Fig. 2a) than at 4 °C. Adult body size of the 12 °C animals was slightly smaller than of animals cultured at 4 °C. Directly after birth, offspring from 4 °C mothers were 31% larger than those from 12 °C mothers (Fig. 2b). The smaller offspring from 12 °C mothers always stayed smaller than the offspring from 4 °C mothers. The absolute difference in body volume between both groups even increased towards the adult age (from $0{\cdot}16 \times 10^6$ µm^3 at birth to $0{\cdot}5 \times 10^6$ µm^3 at the age of 8 days). Figure 3 shows that the size at first reproduction (SFR) was 8% larger in animals cultured at 4 °C *vs* 12 °C animals (environmental effect). The SFR of animals whose mothers were cultured at 4 °C were even 21% larger than in animals from 12 °C mothers (maternal effect). Thus, both the direct environmental effect and the maternal effect of temperature on SFR were significant (Student's *t*-test, $P < 0{\cdot}05$).

The environmental and maternal effects of temperature on egg size in the F1 generation are shown in Fig. 4. When *Synchaeta* (from 8 °C mothers) were cultured at 4 °C, they laid eggs that were on average 25% larger than those of animals cultured at 12 °C

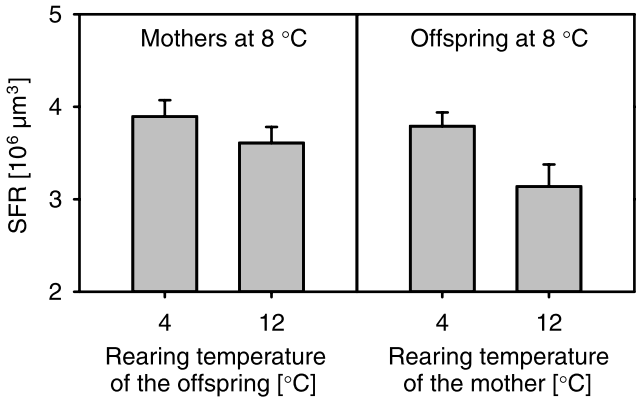

Fig. 3. Size at first reproduction (SFR) of *Synchaeta pectinata* at different temperatures. Left: environmental effect of temperature, i.e. all animals were offspring of mothers cultured at 8 °C and were subsequently cultured at 4 °C or 12 °C. Right: maternal effect of temperature, i.e. all animals were cultured at the same temperature (8 °C) but originated from mothers cultured at 4 °C or 12 °C. Means and standard deviations.

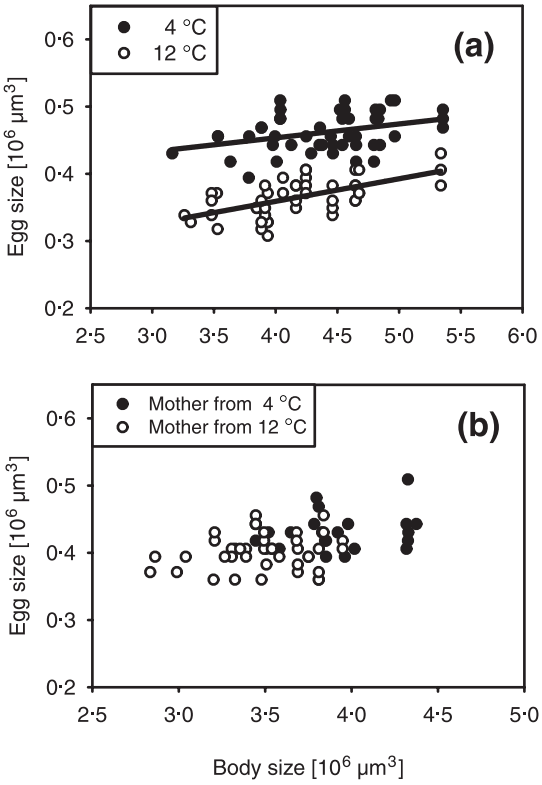

Fig. 4. Factors influencing the size of eggs produced in the F1 generation of *Synchaeta pectinata*: (a) rearing temperature of the F1-generation (direct effect of temperature); mothers of both groups were cultured at 8 °C; (b) rearing temperature of the mother (maternal effect of temperature); both groups (F1) were cultured at 8 °C.

(Fig. 4a). Egg size was correlated to maternal body size as both regression slopes in Fig. 4(a) were significantly different from zero ($P < 0{\cdot}05$). Despite this influence of body size, egg size was highly influenced by the rearing temperature (ANCOVA; $F_{1,89} = 286{\cdot}9$; $P < 0{\cdot}001$). The maternal effect of temperature on egg size was investigated in offspring from 4 °C and 12 °C mothers subsequently cultured at 8 °C (Fig. 4b). If these animals came from 4 °C mothers, they were larger in body size and they laid eggs that were 9% larger (Student's *t*-test, $P < 0{\cdot}001$). Indeed, the differences in body size seemed to explain most of the differences in egg size, as a regression line fitted through all data in Fig. 4(b) had a positive slope ($P < 0{\cdot}05$). Moreover, after adjusting egg sizes for the differences in body sizes, the initial difference between the two groups became non-significant.

The results of the life table response experiments are summarized in Fig. 5. At high food concentrations there were no significant differences in the population growth rate between large eggs (produced by 4 °C mothers) and small eggs (produced by 12 °C mothers) at either temperature. However, at low food concentrations offspring from small eggs had a significantly higher population growth rate than offspring of large eggs when growing at 12 °C ($P < 0{\cdot}05$). Elasticity analysis showed that these differences were mainly due to a higher fecundity in the early adult life (6th and 7th days) in the smaller offspring (see Fig. 6, lower right). At 4 °C, offspring of large eggs had a higher population growth rate than offspring of small eggs. However, this difference was not significant.

Discussion

Previous studies on 'Bergmann's rule' in ectotherms have used both theoretical and empirical approaches. Much theoretical work has been based on the growth equation of Von Bertalanffy:

$$l(t) = l_{\infty}(1 - ce^{-kt}) \qquad \text{eqn 1}$$

where l_{∞} and k are parameters representing asymptotic size and growth coefficient, respectively, c is a parameter relating to initial size, and e is the base of the natural logarithm. Initial size is usually considered constant; therefore the implicit assumption is that differences in adult body size are the result of growth patterns during the juvenile phase (Berrigan & Charnov 1994; Perrin 1995; Atkinson & Sibly 1997). My results with the rotifer *Synchaeta* suggest that this view may be too narrow, since adult body size can be influenced to a great extent by the size of the zygote (egg). Specifically, offspring from smaller eggs (produced at high temperatures) could not catch up in body size with those from larger eggs, not even when they were cultured in unlimited food concentrations. In their review, Atkinson *et al.* (2001) suggest that the production of larger offspring at low temperatures may be a general phenomenon. My results on *Synchaeta pectinata* add another example to their list of studies where possibly confounding variables, such as maternal size, have been accounted for. However, to my knowledge, this is the first study that shows that such temperature-induced changes in offspring size can substantially influence adult body size, even more so than developmental

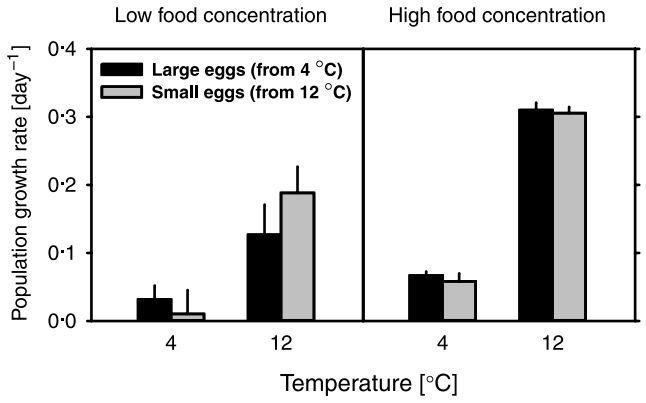

Fig. 5. Population growth rates of large (4 °C eggs) *vs* small offspring (12 °C eggs) at different temperatures and food concentrations. Left: low food concentrations (0·3 mg °C l^{-1}). Right: high food concentrations (3 mg °C l^{-1}). Error bars are jack-knife estimates of the 95% confidence intervals.

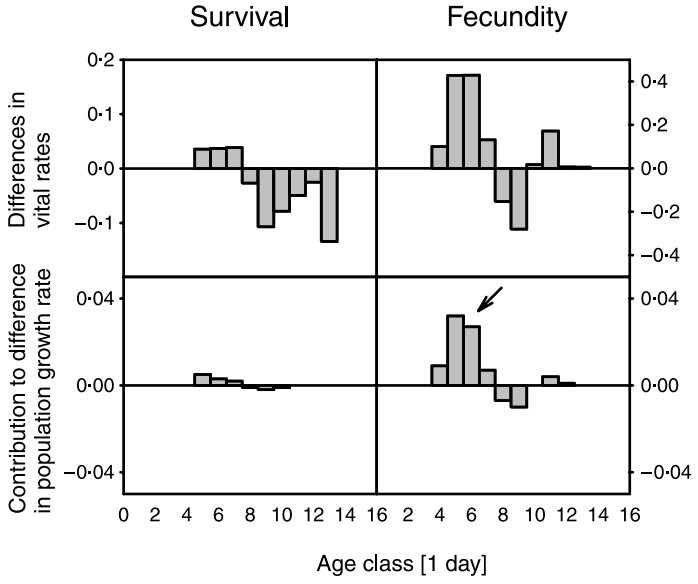

Fig. 6. Results of the sensitivity analysis for small offspring *vs* large offspring at 12 °C/ low food concentrations. Top row: absolute differences in survival and fecundity rates between small and large offspring. Bottom row: contributions of these differences to the observed difference in the population growth rate. The arrow indicates the vital rates that had the highest influence in the difference in the population growth rate.

temperature (see Fig. 3). It is likely that this applies to other organisms as well. For instance, in *Daphnia* the size at first reproduction is strongly influenced by the size at birth. Large neonates mature at larger sizes, while small neonates mature at smaller sizes (Tessier & Consolatti 1989; Lampert 1993). Variation in offspring size in these studies was due to different food concentration or the age of the mothers. As maternal allocation to individual offspring seems to be important in determining adult body size, the currently strong focus on processes of growth/differentiation during the juvenile phase may be viewed with some caution.

Nevertheless, growth during the juvenile phase additionally contributed to the differences in adult size in *Synchaeta*, although to a lesser extent (see Fig. 3). Thus, both processes, the maternal and the direct effect of temperature, contributed to an increased adult body size at low temperatures. It is likely that both processes interact, allowing body size in *Synchaeta* to increase gradually over several parthenogenetic generations. In such a scenario, initially most parental animals would be relatively small in body size but respond to a decrease in temperature by producing larger eggs. The small body size of the parental animals may still constrain the size of their eggs (this is evident from the positive relationship between body size and egg size; see Fig. 4). However the larger F1 animals may be partly released from this constraint. Thus, they can lay larger eggs, which result in even larger F2 animals. Such positive feedback may contribute to relatively strong shifts in body size that can occur in field situations within a few weeks (Green 1998).

A large body size may be adaptive at low temperatures (and a small body size at high temperatures). Two possibilities must be distinguished in this respect. First, the response may be adaptive to environmental factors that are associated with the temperature change. For instance, the demographic model of Yampolsky & Scheiner (1996) suggests that the production of few, large offspring can be adaptive in the face of prolonged exposure to mortality factors, which may be the case at lower temperatures since developmental times are longer. A second possibility is that the change in body size is adaptive to temperature itself. This would mean that large offspring have higher fitness at low temperatures (and the same for small offspring at high temperatures) – all else being equal.

This hypothesis was tested in the present paper. At low and energetically more challenging food concentrations I found that *Synchaeta*, which hatched from small eggs had a higher population growth rate at high temperatures. The effect was mainly caused by higher fecundity in early adult age classes. Offspring from large eggs did not have a significantly higher population growth rate at low temperatures. At high food concentrations there were no differences in the population growth rate of animals that hatched from differentially sized eggs. This result was expected, since a benign environment should pose less selective pressures on individuals. Despite the advantage of small offspring at high temperatures, the results from *Synchaeta pectinata* do not support the hypothesis that the changes in egg size along a temperature gradient are adaptive to temperature itself. A similar result was found in a recent study on parental temperature effects in *Drosophila melanogaster*. Offspring from parents reared at high temperatures were always fitter (in terms of the per capita rate of population increase) than offspring from parents reared at low temperatures (Gilchrist & Huey 2001). These differences were mainly because offspring from hot parents developed more quickly.

Other studies that test the adaptive significance of Bergmann's rule in ectotherms have been done mainly with *Drosophila*. Nunney & Cheung (1997) found that large flies (reared at 18 °C) and small flies (reared at

25 °C) did not differ in their lifetime fecundity. However, at a given temperature, early fecundity was highest when rearing and test temperatures were the same. The fecundity advantage was 25% at 18 °C and 16% at 25 °C, respectively. Another study showed that large male *Drosophila*, artificially selected for at low temperatures, had higher fitness at all temperatures (Reeve, Fowler & Partridge 2000). However, the difference between large and small males was greater at the lower experimental temperature. Both studies support the hypothesis that large body size can be adaptive to temperature itself.

Adaptive adjustment of egg size or newborn size has been reported for other environmental factors as well, such as size-selective predation or food limitation. For example, large offspring can be advantageous if a predator has difficulties in handling large prey items. At low food concentrations it can be adaptive to produce large offspring since these are usually better protected against starvation (Tessier & Consolatti 1989; Kirk 1997). However, in case of temperature it is quite difficult to explain why large ectotherms should have an advantage at low temperature (or why small ectotherms should have an advantage at high temperatures). My results from *Synchaeta* suggest that small individuals use a limiting resource more efficiently at higher temperatures. In order to further clarify the mechanisms behind these patterns, promising directions for future research would be measurements of various metabolic rates (ingestion, respiration) of large *vs* small individuals at different temperatures.

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