



# Breaking the temperature-size rule: Thermal effects on growth, development and fecundity of a crustacean from temporary waters



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## ARTICLE INFO

### Article history:

Received 4 November 2013

Received in revised form

19 February 2014

Accepted 24 February 2014

Available online 4 March 2014

### Keywords:

Development

Fecundity

Growth

Temperature-size rule

Intermoult period

Ostracoda

## ABSTRACT

The temperature-size rule (TSR) is a well-established phenomenon to describe the growth response of ectotherms to temperature by which individuals maintained at low temperatures grow more slowly, but attain a larger size upon maturity. Although there are adaptive and non-adaptive theories about the plasticity of body size in response to temperature, these cannot be applied to all ectotherms, and little is known about the changes in growth and development rates through ontogeny. The ostracod species *Heterocypris bosniaca*, an inhabitant of freshwater temporary ponds, was used to examine the growth and development rates of its nine growth stages and female fecundity at four different temperatures (15 °C, 20 °C, 25 °C and 30 °C). The development rate of this species accelerates with increasing temperature, reaching a maximum value at 25 °C. The growth factor has a reverse-TSR in younger instars, and the typical TSR is followed only in the last two moults, resulting in non-monotonic response of adult size to temperature. Fecundity (total offspring per female) was not directly related to adult size and was generally higher at lower temperatures. Our results agree with recent research showing that the TSR may vary during ontogeny, and may not be a general trend in ostracod species from temporary waters. Indeed, adult carapace size seems to follow the pattern of a thermal reaction norm, probably influenced by the reduction of oxygen bioavailability at low temperature and the drastic increase in metabolic demand at the upper extreme of the thermal gradient.

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## 1. Introduction

The age and body size of individuals are probably the most important features in the life history of organisms. Both are critical because they affect all aspects of life, from anatomical and physiological to ethological and ecological (Forster et al., 2011; Walters and Hassall, 2006). Therefore, understanding the mechanisms regulating the development and body size of organisms is of vital importance in ecology.

Given the lack of consistently thermogenic mechanisms in ectotherms, growth and development strongly depend on ambient temperature. Most studies have shown that ectotherms grow faster at higher temperatures, but that attained size is smaller than at lower temperatures (Atkinson, 1994; Atkinson and Sibly, 1997; Hartnoll, 2001). This is a widely documented phenomenon, called the temperature-size rule (TSR). The diversity of TSR trends is important when considering that variations in body size are among the most sensitive indicators of minor changes in environmental temperature (Hoog and Williams, 1996) and are considered as a universal ecological

response to climate change in aquatic systems (Daufresne et al., 2009). However, it is not clear what kind of general physiological mechanisms might regulate it (Kingsolver and Huey, 2008) and whether or not the same pattern is always shown during ontogenetic development (Forster et al., 2011). In addition, it is unclear whether this response is an adaptation, a product of physiological limitations (Walters and Hassall, 2006), or a combination of multiple factors (Angilletta et al., 2004).

Among the initial attempts to explain the TSR from a physiological point of view, the models of Von Bertalanffy (1960) and Perrin (1995) postulated that anabolism is less thermally dependent than catabolism. Oxygen is essential to maintain metabolism in aerobic organisms, and aquatic ectotherms are especially sensitive to limitations in the availability of oxygen because its diffusion profoundly depends on ambient temperature (Pörtner, 2002a). A remarkable hypothesis based on Pörtner's (2002b) ideas is the "maintain aerobic scope-regulate oxygen supply" (MASROS) by Atkinson et al. (2006), which point out that metabolic rate increases more dramatically with temperature than does oxygen supply. This hypothesis is consistent with the "oxygen supply index" (OSI) proposed by Verberk et al. (2011), who showed that oxygen exchange between aquatic organisms and the environment is driven by an interplay between solubility, diffusivity and partial pressure and results in an increased availability of oxygen

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at warmer temperatures, but the rise in oxygen demand of organisms with temperature eventually exceeds this supply. This situation can lead to oxygen limitation at warmer temperatures that would be more likely to occur in larger individuals (higher oxygen demand) with reduced mechanisms for oxygen uptake and circulation. Alternatively, Angilletta and Dunham (2003) proposed that the TSR could arise from a constraint on growth rate that arises late in ontogeny, i.e. decreasing the thermal optimum for growth efficiency with increasing body size. Although wide support is found for the TSR, some species do not follow it, either because they do not show variations in body size or because they reach larger sizes at higher temperatures (Atkinson, 1995; Hartnoll, 1982). Walters and Hassall (2006) suggested that ectotherms that obey the TSR can be identified as having a higher minimum temperature threshold for development rate than for growth rate. However, more recently Zuo et al. (2012) proposed an energetic fractionation model to account both for TSR and reverse-TSR depending on imbalances in the energy allocated to somatic growth or to maintenance and development.

There is no doubt that, irrespective of the underlying physiological mechanisms regulating the thermal effects on body size, this response variable has strong implications on the evolution of life histories (Stearns, 1992; Angilletta, 2009). Many findings point indeed to selective pressures for increasing body size (Kingsolver et al., 2004), despite the existence of counteracting trade-offs. In this context, Kingsolver and Huey (2008) discussed three rules relating to body size, temperature and fitness: (i) *Bigger is better* (i.e. fitness is higher at larger body size), (ii) *Hotter is smaller* (growth temperature relates negatively to adult body size) and (iii) *Hotter is better* (higher optimal temperatures produce greater maximal performances). These authors found strong support for the *Bigger is better* and *Hotter is smaller* assumptions, but not that much for the third rule. They conclude that complex relationships arise from thermal effects on development of time and growth, and consequently on survival and fecundity, making fitness estimation, as related to temperature, a difficult task.

Discontinuous growth of crustaceans is divided into two components (Hartnoll, 1982): increase in body size (moult increment in absolute terms and the growth factor in relative ones) and time from one moult to the next (intermoult period). Ostracod growth is characterised by a series of moults until the final ecdysis, during which sexual maturity is reached. There are many ecological factors that can affect growth and development (Alcorlo et al., 1999; Hart and Bychek, 2011; Hartnoll, 2001; Juárez-Franco et al., 2009), but temperature is considered as the dominant one in ostracods (Kesling, 1951; Schreiber, 1922). In these organisms, the developmental rate decreases with lower temperatures in natural populations and under laboratory conditions (Ganning, 1971; Latifa, 1987; Mezquita et al., 1999; Roca and Wansard, 1997), while adult size does not present a clear monotonic response to temperature (Liberto et al., 2013; Martens, 1985). This scenario demonstrates that ostracods undergo accelerated development with increasing temperatures, but they do not always follow the TSR, as is also the case in other crustaceans (Hartnoll, 2001).

*Heterocypris bosniaca* is a poorly known species of ostracod. It was discovered in 2000 in Bosnia (Petkowski et al., 2000) and since then it has only been reported in Israel (Martens et al., 2002) and Spain (Aguilar-Alberola and Mezquita, 2008). In previous studies on its population dynamics in two small temporary rockpools in eastern Spain we observed that the species has a multi-voltine life cycle adapted to the unpredictability of these stressful environments (Aguilar-Alberola and Mesquita-Joanes, 2011). The main dry phase occurs in summer and the resting egg bank enables the continuity of the species in the rockpools. We also observed variations in the intermoult period among different cohorts; they developed faster at higher temperatures in fall than

during cold winter months, which match the expected relationship between development rate and temperature within the TSR framework. For this reason, we decided to analyse the response of the species under controlled laboratory conditions in detail to check if warmer temperature had the effect of development acceleration observed in natural populations and whether or not this ostracod species followed the TSR pattern.

This paper analyses the effects of temperature on development rate, size changes at each developmental instar and adult fecundity and survival of a multivoltine ostracod living in temporary water bodies. This allows evaluating physiological issues like the validity of the TSR through ontogeny in aquatic ectotherms with determinate growth. Understanding the length pattern in adults can help us to find out if it fits the expectations of recent physiological theories such as the effects on growth of the balance between oxygen bioavailability and its metabolic uptake, as proposed by Verberk et al. (2011) and others. Furthermore, we can also relate differential temperature effects on growth and development to fitness components such as fecundity and survival, in order to test whether or not adaptive aspects such as the assumptions *Bigger is better* and *Hotter is smaller* (Kingsolver and Huey, 2008) hold in this group of organisms adapted to quickly changing environments.

## 2. Materials and methods

The ostracods used for this study were collected in a small (92 × 120 cm, maximum depth 20 cm) temporary pond in eastern Spain (rockpool “X6” in Aguilar-Alberola and Mezquita (2008); coordinates 39°02'51"N 0°26'14"W). In the previous field study by Aguilar-Alberola and Mesquita-Joanes (2011), the main hydroperiod of this pond lasted for 23 weeks, from September 2005 to March 2006. During this period water temperature measured during the day averaged 13.7 °C, ranging from a minimum value of 6.5 °C to a maximum of 27 °C, but the average air temperature in the area was 11.4 °C, varying between –4.4 °C and 31.7 °C. Individuals (all parthenogenetic females) were captured using a small hand net, and were transported to the laboratory and divided into four 1.5 L aquaria with filtered water from the pond to set stock cultures. The four aquaria were kept in growth chambers at constant temperatures of 15 °C, 20 °C, 25 °C and 30 °C each and under a photoperiod of 12:12 h. Cultures were provided with food every 2–3 days, which alternated between insect homogenate and dried *Spirulina* sp. The water level was kept constant by the addition of distilled water when required. Under these conditions, stock cultures were maintained until ostracods had acclimatised to the temperature and a new cohort of individuals had appeared in the aquaria.

In order to determine the intermoult period at different temperatures, the ostracods belonging to early developmental instars were individually isolated in 2 mL multi-well plates and maintained in the same temperature, photoperiod and food supply conditions as those in the stock cultures. All the individuals in the multi-well cultures were checked every 12 h (the first two juvenile instars A-8 and A-7) or 24 h (instars A-6 to adult), for a period of observation of 10 s, for survival and moulting. Due to the fragility and short duration of stage A-9 (no longer than 2 min at 25 °C; Aguilar-Alberola and Mesquita-Joanes, 2013), the present survey does not take this stage into account. With each observation event, individuals' status (alive/dead) was checked and detached valves were sought to determine on which day the moult (ecdysis) occurred. All the valves and dead individuals were removed from the multi-well plates and they were measured by stereomicroscope observations to calculate the growth factor (growth rate between the instar carapace length after moulting compared with length of the previous instar) and the instar to which they belonged. This enabled the duration of all the instars to be

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