



Temperature adaptation in larval development of lithodine crabs from deep-water lineages

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ABSTRACT

Adaptations in per-offspring investment and larval development are considered to have been crucial to the global radiation of deep-water lineages of lithodine crabs (Lithodinae). Temperature is proposed to drive latitudinal trends in energy provisioning of eggs in marine invertebrates, mediated by thermally dependent intraspecific plasticity in per-offspring investment. Consequently, a changing climate may be expected to directly affect larval provisioning. We analysed available data to examine any differences in per-offspring investment and larval development among deep-water lineage lithodines. Although data are few, interspecific differences in the thermal scope of deep-water-lineage lithodine larvae appear coupled with differences in biogeography. This coupling suggests environmental temperature influences larval thermal scope. Lithodine phylogeography suggests that larval cold-eurythermy in deep-water-lineage lithodines is a derived trait that has evolved in relatively warm and variable subantarctic shallow water. Therefore, we hypothesise that capacity to adapt to warmer and more variable environmental conditions may afford deep-water-lineage lithodines some resilience to ocean warming, depending on the rates of environmental and adaptive change. Interspecific comparisons also suggest that larval duration and per-offspring investment are positively correlated. Faster development at a given temperature is associated with higher respiration rates and greater energetic reserve utilisation. Therefore, we hypothesise that selection pressure for contrasting metabolic adaptations in different thermal environments contributes to shifts in larval duration and per-offspring investment.

1. Introduction

Lecithotrophic (food-independent) larval development is associated with high quantity and quality of maternal resources allocated to each individual offspring to fuel development (per-offspring investment) (Anger, 2001; Oliphant and Thatje, 2013). High per-offspring investment and lecithotrophy are also linked with abbreviated development, where larvae proceed through relatively few larval stages before metamorphosis to juvenile (Anger, 2001). Egg size is a proxy for energy provisioning and typically increases with latitude (Marshall et al., 2012). Temperature has long been proposed as an important factor driving latitudinal trends in energy provisioning of eggs in marine invertebrates (Thorson, 1936). Intraspecific investigations have found that energy allocation influences larval development and mediates adverse effects of temperature on larval development (Giménez, 2006; Oliphant et al., 2013; Oliphant and Thatje, 2013; Gonzalez-Ortégón and

Giménez, 2014). Consequently, temperature has been thought to drive energy allocation to offspring. Thermal plasticity in per-offspring investment within species putatively emerges from differing temperature effects on oogenesis and vitellogenesis that result in increased energy allocation to eggs at lower temperatures (Van der Have and De Jong, 1996; Oliphant and Thatje, 2013). Consequently, a changing climate may have direct impacts on larval provisioning.

Sea surface temperature is predicted to reach between 1 °C and 3 °C higher in the period 2081–2100 than in the period 1986–2005 (Collins et al., 2013) and thermal variability is expected to increase significantly (Lima and Wetthey, 2012). Polar marine taxa are predicted to experience the greatest challenge due to adaptation to low temperature and poleward constraints on biogeographic range (Parmesan, 2006; Brown and Thatje, 2015). Although average sea surface temperature is predicted to rise faster than temperature in deeper waters, the whole ocean will warm up reasonably uniformly eventually (Li et al., 2013). Deep-

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water taxa are typically adapted to constant low temperature (Brown and Thatje, 2014) and will therefore be exposed to significant challenge, too. Exploring interspecific differences in larval development in a cold-adapted family of marine decapod crustaceans with polar or deep-sea distribution may reveal potential for adaptation to increasing temperature and increasing temperature variability.

The cold-adapted lithodine crabs occur throughout the deep sea and in shallow waters at subpolar latitudes. Phylogeographic analysis indicates that lithodines originated in shallow waters in the Northeast Pacific before colonising the deep sea and re-emerging in polar environments (Hall and Thatje, 2009, 2018). The lithodine radiation occurred relatively rapidly, beginning in the late Miocene ~15 Mya (Makarov, 1962; Zaklan, 2002a, 2002b; Hall and Thatje, 2009; Snow, 2010; Bracken-Grissom et al., 2013). Lithodine species that remain restricted to shallow water (< 300 m depth) in the North Pacific are predominantly planktotrophic, whereas deep-sea and polar species (deep-water lineages) are obligate lecithotrophs (see Hall and Thatje, 2009). Although lecithotrophy (inferred from egg size > 1.2 mm in lithodids) appears to have evolved in 2 species of *Paralithodes* that remain restricted to the shallow North Pacific (Snow, 2010), adaptations in larval development mode are considered the key feature that enabled deep-sea colonisation by the Lithodinae and re-emergence in polar environments (Thatje et al., 2005).

Shallow-water lithodines endemic to the North Pacific develop through 4 zoeal stages prior to megalopa, whereas deep-sea and polar lithodines develop through only 3 (*Lithodes* spp.) or 2 (*Paralomis* spp.) zoeal stages before reaching the megalopa (Zaklan, 2002b). The number of larval stages decreases with increasing latitude and increasing depth in lithodines (see Zaklan, 2002b). In contrast, both per-offspring investment and the duration of larval stages increase with increasing latitude and increasing depth (see Zaklan, 2002b; Thatje and Hall, 2016). Such interspecific macroecological trends suggest that lecithotrophy, increased per-offspring investment, abbreviated development, and increased larval duration in lithodines are derived evolutionary adaptations (Anger, 2001; Thatje et al., 2005; Hall and Thatje, 2009; Thatje and Hall, 2016). These adaptations have likely arisen in response to unpredictable or low food availability and/or the mismatch between short periods of primary production that result from extreme seasonality, and prolonged development at high latitudes or in deep water that results from low temperature (Anger, 2001, Thatje et al., 2005, Hall and Thatje, 2009, Thatje and Hall, 2016).

The aim of this study is to utilise available data to examine differences in adaptations in larval development among deep-water lineage lithodines inhabiting contrasting thermal environments, elucidating potential for deep-water lineage lithodines to adapt to increasing temperature and temperature variability, and highlighting larval development traits and per-offspring investment traits potentially positively selected by temperature.

2. Materials and methods

2.1. Literature search

The literature was searched using the ISI Web of Science database and the Google Scholar search engine employing “temperature”, “lecithotroph”, “larval”, “development”, “lithodid”, and “lithodine” as keywords. Developmental duration, dry mass, C mass, N mass, C:N ratio, and respiration rate data were extracted from seven publications reporting lecithotrophic larval development in lithodid species from deep-water lineages (*Lithodes aequispinus*, *Lithodes maja*, *Lithodes santolla*, *Paralomis granulosa*, and *Paralomis spinosissima*) (Paul and Paul, 1999; Anger et al., 2003, 2004; Calcagno et al., 2003; Lovrich et al., 2003; Thatje and Mestre, 2010; Brown et al., 2018).

2.2. Larval thermal scope

Larval thermal scope was assessed as the range of experimental temperatures at which larvae successfully developed to juvenile. Sufficient data were available to assess larval thermal scope in *L. maja*, *L. santolla*, and *P. granulosa* (Anger et al., 2003, 2004; Brown et al., 2018). Larvae developed to juvenile successfully in *L. aequispinus* at all three temperatures examined (3, 6, and 9 °C) (Paul and Paul, 1999) and larval development in *P. spinosissima* was examined at a single temperature (5 °C) (Thatje and Mestre, 2010), therefore it was not possible to assess larval thermal scope in these species.

2.3. Larval duration and the effects of temperature on larval duration

Interspecific differences in zoea I duration and in the effect of temperature on the duration of zoea I were assessed using ANCOVA with mean zoea I duration data. Sufficient data were available to include *L. aequispinus*, *L. maja*, *L. santolla*, and *P. granulosa* in the analysis (Paul and Paul, 1999; Anger et al., 2003, 2004; Brown et al., 2018). Larval development in *P. spinosissima* was examined at 5 °C only. (Thatje and Mestre, 2010).

2.4. Larval mass measures

Interspecific differences in larval mass measures in zoea I at hatching were assessed using ANOVA. Sufficient data were available to include *L. maja*, *L. santolla*, *P. granulosa* and *Paralomis spinosissima* in the analysis (Calcagno et al., 2003; Lovrich et al., 2003; Thatje and Mestre, 2010; Brown et al., 2018). Only mean zoea I dry mass was available for *L. aequispinus*, but without identifiable n, preventing inclusion in the analysis (Shirley and Zhou, 1997).

Changes in larval mass parameters in *L. maja*, *L. santolla*, and *P. granulosa* during larval development at 6 °C were described with linear regressions as functions of mean larval duration and compared using ANCOVA. Larval mass parameter data from *P. spinosissima* were only available from larval development at 5 °C and were therefore excluded.

Whilst statistical comparisons of larval mass parameters may reveal significant differences in larval development among species, these cannot be unequivocally attributed to interspecific differences: differences may result from contrasting environmental or experimental conditions.

2.5. Covariance in larval dry mass and duration

Interspecific covariance in zoea I dry mass and zoea I duration was examined by testing the correlation (Pearson product-moment correlation) between mean zoea I dry mass and mean zoea I duration at 5 °C. Selecting 5 °C allowed inclusion of *P. spinosissima* zoea I duration and zoea I dry mass data (Thatje and Mestre, 2010). Zoea I duration in *L. maja*, *L. santolla*, and *P. granulosa* at 5 °C were calculated from temperature-duration functions (Table 1). Covariance in zoea I dry mass

Table 1

Fitted parameters (a, b) and coefficients of determination (r^2) of non-linear power regression eqs. ($D = a \times T^b$) describing mean development duration (D, days) of different components of larval development as a function of temperature (T, °C); recalculated from sources.

Stage(s)	Species	a	b	r^2	Source
Zoea I	<i>Lithodes aequispinus</i>	26.4	-0.660	1.000	Paul and Paul (1999)
	<i>Lithodes maja</i>	37.8	-0.811	0.988	Brown et al. (2018)
	<i>Lithodes santolla</i>	17.9	-0.679	0.971	Anger et al. (2004)
	<i>Paralomis granulosa</i>	16.9	-0.685	0.997	Anger et al. (2003)
Larval	<i>Lithodes aequispinus</i>	299.5	-0.641	0.994	Paul and Paul (1999)
	<i>Lithodes santolla</i>	450.6	-1.080	0.995	Anger et al. (2004)
	<i>Paralomis granulosa</i>	349.8	-0.993	0.995	Anger et al. (2003)

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