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

Alastair Brown1\*, Sven Thatje1, Andrew Oliphant1,2, Catriona Munro1,3, Kathryn E. Smith1,4

1Ocean and Earth Science, University of Southampton, National Oceanography Centre Southampton, European Way, Southampton, SO14 3ZH, UK

2*present address* Institute of Biological, Environmental & Rural Sciences, Aberystwyth University, Penglais, Aberystwyth, Ceredigion, SY23 3FG, UK

3*present address* Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA

4*present address* College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4QD, UK

\*[alastair.brown@noc.soton.ac.uk](mailto:alastair.brown@noc.soton.ac.uk)

**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.

**Key words:** early ontogeny; lecithotrophy; lithodid; per-offspring investment; thermal scope**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-Ortegón 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 & de Jong 1996, Oliphant & 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 Wethey 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-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,b, Hall and Thatje 2009, Snow 2010, Bracken-Grissomet 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**

*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).

*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.

*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).

*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.

*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 and total larval duration (hatching to metamorphosis) was also examined by testing the correlation between mean zoea I dry mass and total larval duration at 5°C to allow the inclusion of *P*. *spinosissima* data (Thatje and Mestre 2010). Total larval duration in *L*. *santolla* and *P*. *granulosa* were calculated from temperature-duration functions (Table 1), but insufficient data prevented derivation of a temperature-duration function for total larval durationin *L*. *maja* (Brown et al. 2018).

*Phylogenetic independent contrasts*

A phylogenetic tree was generated using combined 16S, 28S, COI and ITS1 data available in GenBank and used by Snow (2010). Sequences were aligned using MAFFT (version 7.017). A maximum likelihood tree was generated using the GTR+Γ nucleotide substitution model in RAxML (version 8.2.8) and 1000 bootstraps. The maximum likelihood tree was pruned to consider only the species with trait data.

Phylogenetic independence of larval mass measures was assessed using the pruned ultrametric tree and Moran’s autocorrelation coefficient (Paradis 2016). Phylogenetic independence of covariance in mean zoea I dry mass and mean zoea I duration, and mean zoea I dry mass and mean larval duration were assessed using the pruned ultrametric tree and the R package ape (version 3.5) (Paradis et al. 2004). To test sensitivity of the phylogenetic independent contrasts to branch length, branch lengths were simulated 100 times and contrasts were calculated on trees with simulated branch lengths.

The maximum likelihood tree did not have high bootstrap support for many of the nodes. Further, only a limited number of species had available trait data (4-5 depending on parameter). The resulting phylogenetic independence contrasts must therefore be interpreted cautiously and used to suggest potential hypotheses for testing rather than definitive conclusions.

**3. Results**

*Larval thermal scope*

Larval thermal scope differed among lithodine species. Larval thermal scope was 6°C to 9°C for *Lithodes maja* (Brown et al. 2018) and 3°C to 15°C for *L*. *santolla* (Anger et al. 2004) and *P*. *granulosa* (Anger et al. 2003)

*Larval duration and the effects of temperature on larval duration*

The effect of temperature on zoea I duration did not differ significantly among the *Lithodes* species compared(F2,10 = 2.062, p = 0.178). In contrast, zoea I duration differed significantly among species of *Lithodes* (F2,12 = 16.296, p < 0.001); zoea I duration did not differ significantly between *L. aequispinus* and *L*. *maja* (F1,6 = 0.010, p = 0.925), but was significantly shorter in *L*. *santolla* than in both those species (respectively, F1,7 = 20.564, p = 0.003 and F1,10 = 23.830, p < 0.001). Similarly, zoea I duration was significantly shorter in *Paralomis granulosa* than in *L*. *aequispinus* and *L*. *maja* (respectively, F1,6 = 100.783, p < 0.001 and F1,8 = 14.001, p = 0.006), but did not differ significantly from zoea I duration in *L*. *santolla* (F1,10 = 0.003, p = 0.958).

*Larval mass measures*

Zoea I dry mass, C mass, N mass, and C:N ratio were significantly greater in *P*. *spinosissma* than in the other deep-water lineage lithodine species (p < 0.05). Similarly, zoea I dry mass, C mass, N mass, and C:N ratio were significantly greater in *L*. *maja* than in *L*. *santolla* or *P*. *granulosa* (p < 0.05). Zoea I dry mass, C mass, and N mass did not differ significantly between *L*. *santolla* and *P*. *granulosa* (p > 0.05), but C:N ratio was significantly greater in *L*. *santolla* (p < 0.05).

The rate of decrease in dry mass, C mass, N mass, and C:N ratio did not differ significantly between *L*. *maja* and *L*. *santolla* (Fig. 1) (respectively, F1,6 = 0.001, p = 0.973; F1,6 = 0.110, p = 0.751, F1,6 = 0.093, p = 0.770, and F1,6 = 2.190, p = 0.189) or between *L*. *maja* and *P*. *granulosa* (respectively, F1,5 = 0.426, p = 0.543; F1,5 = 0.159, p = 0.707, F1,5 = 2.424, p = 0.180, and F1,5 = 1.024, p = 0.358). Consequently, dry mass, C mass, N mass, and C:N ratio overall were significantly greater in *L*. *maja* than in *L*. *santolla* (respectively, F1,7 = 27.042, p = 001; F1,7 = 11.758, p = 0.011, F1,7 = 17.597, p = 0.004, and F1,7 = 13.151, p = 0.008) or *P*. *granulosa* (respectively, F1,6 = 31.181, p = 0.001; F1,6 = 19.105, p = 0.005, F1,6 = 14.749, p = 0.009, and F1,6 = 38.154, p < 0.001).

In contrast, whilst the rate of decrease in dry mass, C mass, and C:N ratio did not differ significantly between *L*. *santolla* and *P*. *granulosa* (respectively, F1,5 = 1.508, p = 0.274, F1,5 = 1.344, p = 0.299, F1,5 = 0.043, p = 0.844), the rate of decrease in N was significantly greater in *P*. *granulosa* (F1,5 = 15.75, p = 0.011). Dry mass overall did not differ significantly between *L*. *santolla* and *P*. *granulosa* (F1,6 = 5.411, p = 0.059), but C mass and C:N ratio overall were significantly greater in *L*. *santolla* (respectively, F1,6 = 5.989, p = 0.050, F1,6 = 29.712, p = 0.002).

Crab I dry mass, C mass, N mass, and C:N ratio were significantly greater in *L*. *maja* than in *L. santolla* and *P*. *granulosa* (p > 0.05). Although Crab I C mass and N mass ratio were significantly greater in *L*. *santolla* than in *P*. *granulosa*, dry mass and C:N did not differ significantly (p > 0.05).

*Covariance in larval dry mass and duration*

Both zoea I duration and total larval duration at 5°C were significantly positively correlated with zoea I dry mass (Fig. 2) (respectively, r = 0.930, df = 3, p = 0.022; r2 = 0.864 and r = 0.996, df = 2, p = 0.004; r2 = 0.992).

*Phylogenetic independent contrasts*

Moran’s autocorrelation coefficient indicated that the distributions of zoea I dry mass, C mass, N mass, and C:N ratio were not significantly affected by phylogenetic relationships (p > 0.05). Similarly, covariance between zoea I dry mass and zoea I duration, and covariance between zoea I dry mass and total larval duration remained significant when phylogenetic relationships were taken into account (respectively, p = 0.010, r2 = 0.891 and p = 0.002, r2 = 0.994). Results were robust to randomised changes in branch length, with all simulations meeting the following criteria: r2 > 0.6 and p < 0.1 for zoea I duration, and r2 > 0.9 and p < 0.05 for larval duration.

**4. Discussion**

*Larval thermal scope*

The contrast between the broad thermal scope reported for *L*. *santolla* and *P*. *granulosa* (3°C to 15°C) (Anger et al. 2003, 2004) and narrow thermal scope observed in *L*. *maja* (6°C to 9°C) (Brown et al. 2018) suggest differences in thermal adaptation in larval development among deep-water lineage lithodines. The putative deep-dispersal routes of deep-water-lineage lithodines out of the North Pacific site of origin (see Snow 2010) and the biogeography of the examined deep-water-lineage lithodine species suggest that eurythermal cold-adaptation in *L*. *santolla* and *P*. *granulosa* may be a derived trait representing adaptation to their relatively warm and variable subantarctic shallow-water environment. Both *L*. *santolla* and *P*. *granulosa* occur in the Southeast Pacific and Southwest Atlantic between the intertidal and 100 m at temperatures between 3°C and 18°C, whereas *L. maja* occurs in the North Atlantic at depths from 4 to 790 m at temperatures between 0°C and 10°C (Zaklan 2002b and references cited therein, Anger et al. 2004, Brown et al. 2017). Thus, *L*. *maja* inhabits cooler and more stable waters in the North Atlantic which are more typical of deep-water lineage lithodines. The potential for increased larval thermal scope indicated by the evolution of larval cold-eurythermy in *L*. *santolla* and *P*. *granulosa* suggests that other lithodines may be similarly capable of overcoming the challenges of ocean warming. However, this will depend on rates of environmental and adaptive change. Deep-water lineage lithodines are broadcast spawners with long larval duration. Such strategy offers relatively low capacity for population differentiation and cryptic speciation (Thatje 2012), reducing the potential for rapid adaptation to changing climate.

Exploration of larval thermal tolerances in other deep-water lineage lithodines should be considered a priority for confirming the hypothesis that eurythermal cold-adaptation in deep-water lineage lithodines is a derived trait representing adaptation to a relatively warm and variable environment. Such investigation will support understanding of future biogeographic impacts of changing climate. For example, identifying the larval thermal scope in Antarctic lithodine species may clarify the potential for invasion of Antarctic shelf communities with ocean warming. Lithodines are present on the Antarctic continental slope but are putatively excluded from the Antarctic continental shelf by intolerance of low polar temperatures. Warming ocean temperatures are, therefore, likely to allow biogeographic range extension by lithodines onto the Antarctic continental shelf (Thatje et al. 2005; Hall and Thatje 2011, Aronson et al. 2015, Smith et al. 2017a). Since the Antarctic shelf benthos have evolved in the absence of durophagous (skeleton-crushing) predators over millions of years, invasion by durophagous lithodines would likely result in radical alteration of the shelf community structure (Thatje et al. 2005, Smith et al. 2017a).

*Larval duration and temperature effects on larval duration*

Interspecific differences in larval duration may be mediated by metabolic adaptations. Metabolic rate influences intraspecific variation in the rate of larval development (Brown et al. 2018). Consistent with this, metabolic rate in *L*. *maja* zoea Ilarvae was less than half the metabolic rate of faster developing *P*. *granulosa* zoea I larvae at all temperatures examined (1°C to 15°C) (cf. Thatje et al. 2003, Brown et al. 2018). For example, at 6°C *L*. *maja* zoea I metabolic rate was ~10% of *P*. *granulosa* zoea I metabolic rate and *L*. *maja* zoea I duration was ~160% of *P*. *granulosa* zoea I.

Metabolic adaptations that provide the physiological plasticity required to tolerate the seasonally fluctuating, low-temperature, shallow-water environments inhabited by *P*. *granulosa* and *L*. *santolla* are suggested to require greater metabolic rate than metabolic adaptations to the constant low-temperature environments inhabited by *L*. *aequispinus* and *L*. *maja* (Pörtner et al. 2000). Larval development in species adapted to variable low temperature environments will therefore be more rapid than larval development in species adapted to constant low temperature environments at a specific temperature. In contrast, metabolic adaptation to the thermodynamic and physiological effects of colder and constant low-temperature environments such as inhabited by *P*. *spinosissima* is relatively more energetically expensive (e.g. White et al. 2012), increasing basal energy costs: *P*. *spinosissima* is reported from the Southwest Atlantic and Antarctic Ocean between 132 and 650 m depth (Zaklan 2002b). Lower metabolic rate is associated with greater developmental efficiency within a species (Brown et al. 2018) and therefore may be favoured by selection pressure during adaptation to constant low temperature, resulting in slower larval development. Metabolic adaptations to high hydrostatic pressure may also favour decreased metabolic rate and slower development in lithodines from deep-water-lineages. The physiological effects of high hydrostatic pressure reduce energetic efficiency during lecithotrophic development, similar to the effects of low temperature (Smith et al. 2015), and metabolic adaptations to high hydrostatic pressure are typically similar to metabolic adaptations to low temperature (see Brown and Thatje 2014). However, developmental rate (and thus metabolic rate) is likely in a selective trade-off with predation risk and/or risk of advective loss (Pringle et al. 2014), counterbalancing selection pressure for slower and more energetically efficient development.

The inferences made here regarding environmental adaptation are based on few species due to the necessary selection criteria, demanding that conclusions must be treated with caution. However, the only other larval duration data available for lithodines from deep-water lineages appear consistent with this hypothesis. The 17-day mean duration of the zoea I and zoea II in the deep-sea species *Paralomis histrix* at 10.5°C (Konishi and Taishaku 1994) is more than double the 7.9 day mean duration of zoea I and zoea II in *P*. *granulosa* at 12°C (Anger et al. 2003). *P*. *histrix* inhabits the North Pacific between 230 and 600 m (Zaklan 2002b).

*Larval mass measures*

Lecithotrophy in *L*. *santolla* and *P*. *granulosa* may be regarded as an indicator of deep-sea ancestry (Strathmann 1978; Hall and Thatje 2009). However, these species have the lowest energetic reserves at hatching and shortest larval duration known in lithodines from deep-water lineages (Thatje and Mestre 2010). The interspecific macroecological trend of increasing per-offspring investment with decreasing temperature in the Lithodidae (Thatje and Hall 2016) therefore suggests that low per-offspring investment in *L*. *santolla* and *P*. *granulosa* relative to other deep-water lineage lithodines may reflect adaptation to the relatively warm and variable subantarctic shallow waters these species inhabit. Nonetheless, there is little significant difference in the rate of resource utilisation among the examined deep-water lineage lithodines.

*Covariation in larval dry mass and duration*

Selection pressure may favour shifts in per-offspring investment in lithodines from deep-water lineages during adaptation to different low-temperature environments (Morley et al. 2006, Thatje and Hall 2016). Zoea I energetic reserves putatively reflect per-offspring investment (Thatje and Mestre 2010, Oliphant and Thatje 2013). Thus, the correlation between developmental duration and zoea I energetic reserves in lithodines from deep-water lineages suggests simultaneous positive selection in developmental duration and per-offspring investment. However, confirming this hypothesis requires ancestral state reconstruction.

Energetic constraints imply that per-offspring investment is in equilibrium with fecundity in a selective trade-off (Smith and Fretwell 1974). Higher total energetic cost during development in constant-low-temperature environments may increase selection pressure for greater larval energetic reserves and lead to greater per-offspring investment, as observed in *P*. *spinosissima*. In contrast, lower energetic reserve utilisation during development may allow selection pressure for higher fecundity to dominate, leading to lower per-offspring investment (Fischer et al. 2003). Consistent with this hypothesis, per-offspring investment in rapidly developing shallow-water eurythermal *P*. *granulosa* and *L*. *santolla* are the lowest reported among lithodines from deep-water lineages (Thatje and Mestre 2010), and energetic reserve utilisation to metamorphosis is lower in both *P*. *granulosa* and *L*. *santolla* than in *L*. *maja,* despite greater metabolic rate (cf. Fig. 4 Calcagno et al. 2003, Fig. 5 Lovrich et al. 2003, and Fig. 6 Brown et al. 2018). Indeed, *P*. *granulosa* appears to be close to the limits of lecithotrophy (Kattner et al. 2003). Temperature-driven reduction in per-offspring investment may be constrained by the putatively irreversible reduction or loss of complex larval morphology (e.g. mandibles; McLaughlin et al. 2001, 2003) or metabolic function (e.g. digestive enzymes; Saborowski et al. 2006) required for planktotrophic feeding, during the evolution of obligate lecithotrophy (see Strathmann 1978). A transition to planktotrophy in response is therefore unlikely to occur with ocean warming. Other life history adaptations in lithodines from deep-water lineages are likely similarly constrained as a consequence, for example relatively low fecundity (cf. Webb 2014 and references cited therein, Smith et al. 2017b, Brown et al. 2018) and extended hatching periods (cf. Paul and Paul 2001, Thatje et al. 2003, Reid et al. 2007, Brown et al. 2018).

*Conclusions*

Limitations to the phylogenetic independent contrasts, in particular the limited number of species for which trait data were available, demand cautious interpretation of the interspecific relationships reported here. The interspecific relationships have, therefore, been used to propose hypotheses for testing rather than asserting definitive conclusions.

Differences in larval thermal scope among species of deep-water-lineage lithodines appear linked to biogeography. This link suggests that the environmental temperature regime affects larval thermal scope with cold-eurythermy having evolved in species inhabiting relatively warm and variable subantarctic shallow water. Consequently, we hypothesise that deep-water-lineage lithodines may have capacity to adapt to warmer and more variable environmental conditions, depending on the rates of adaptive and environmental change, which may provide some resilience to changing climate.

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 in deep-water lineage lithodines.**Acknowledgements**

AB and ST conceived the work; AB analysed data; CM assessed phylogenetic independence of contrasts; AB drafted the manuscript; all authors contributed to manuscript writing. AB was supported through a Natural Environment Research Council PhD studentship and this study was supported by a grant from ASSEMBLE (FP7) to ST and AB.

**Ethical approval**

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. **References**

Anger, K., 2001. The biology of decapod crustacean larvae. AA Balkema, Lisse.

Anger, K., Thatje, S., Lovrich, G., Calcagno, J., 2003. Larval and early juvenile development of *Paralomis granulosa* reared at different temperatures: tolerance of cold and food limitation in a lithodid crab from high latitudes. Mar. Ecol. Prog. Ser. 253, 243-251.

Anger, K., Lovrich, G.A., Thatje, S., Calcagno, J.A., 2004. Larval and early juvenile development of *Lithodes santolla* (Molina, 1782) (Decapoda: Anomura: Lithodidae) reared at different temperatures in the laboratory. J. Exp. Mar. Biol. Ecol. 306, 217-230.

Aronson, R.B., Smith, K.E., Vos, S.C., McClintock, J.B., Amsler, M.O., Moksnes, P.-O., Ellis, D.S., Kaeli, J., Singh, H., Bailey, J.W., Schiferl, J.C., van Woesik, R., Martin, M.A., Steffel, B.V., Deal, M.E., Lazarus, S.M., Havenhand, J.N., Swalethorp, R., Kjellerup, S., Thatje, S., 2015. No barrier to emergence of bathyal king crabs on the Antarctic shelf. Proc. Nat. Acad. Sci. U.S.A. 112, 12997-13002.

Bracken-Grissom, H.D., Cannon, M.E., Cabezas, P., Feldmann, R.M., Schweitzer, C.E., Ahyong, S.T., Felder, D.L., Lemaitre, R., Crandall, K.A., 2013. A comprehensive and integrative reconstruction of evolutionary history for Anomura (Crustacea: Decapoda). B.M.C. Evol. Biol. 13, 1-28.

Brown, A., Thatje, S., 2014. Explaining bathymetric diversity patterns in marine benthic invertebrates and demersal fishes: physiological contributions to adaptation of life at depth. Biol. Rev. 89, 406-426.

Brown, A., Thatje, S., 2015. The effects of changing climate on faunal depth distributions determine winners and losers. Glob. Change Biol. 21, 173-180.

Brown, A., Thatje, S., Morris, J.P., Oliphant, A., Morgan, E.A., Hauton, C., Jones, D.O.B., Pond, D.W., 2017. Metabolic costs imposed by hydrostatic pressure constrain bathymetric range in the lithodid crab *Lithodes maja*. J. Exp. Biol. 220, 3916-3926.

Brown, A., Thatje, S., Oliphant, A., Munro, C., Smith, K.E., 2018. Temperature effects on larval development in the lithodid crab *Lithodes maja*. J. Sea. Res. 139, 73-78.

Calcagno, J.A., Thatje, S., Anger, K., Lovrich, G.A., Kaffenberger, A., 2003. Changes in mass and chemical composition during lecithotrophic larval development of the southern stone crab *Paralomis granulosa*. Mar. Ecol. Prog. Ser. 257, 189-196.

Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W.J., Johns, T., Krinner, G., Shongwe, M., Tebaldi, C., Weaver, A.J., Wehner, M., 2013. Long-term climate change: projections, commitments and irreversibility. In: Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (eds) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the International Panel on Climate Change. Cambridge University Press, Cambridge, p. 1029-1136.

Fischer, K., Brakefield, P.M., Zwaan, B.J., 2003. Plasticity in butterfly egg size: why larger offspring at lower temperatures? Ecology 84, 3138-3147.

Giménez, L., 2006. Phenotypic links in complex life cycles: conclusions from studies in decapod crustaceans. Integr. Comp. Biol. 46, 615-622.

Gonzalez-Ortégon, E., Giménez, L., 2014. Environmentally mediated phenotypic links and performance in larvae of a marine invertebrate. Mar. Ecol. Prog. Ser. 502, 185-195.

Hall, S., Thatje, S., 2009. Global bottlenecks in the distribution of marine Crustacea: temperature constraints in the family Lithodidae. J. Biogeogr. 36, 2125-2135.

Hall, S., Thatje, S., 2011. Temperature-driven biogeography of the deep-sea family Lithodidae (Crustacea: Decapoda: Anomura) in the Southern Ocean. Polar Biol. 34, 363-370.

Hall, S., Thatje, S., 2018. Evolution through cold and deep waters: the molecular phylogeny of the Lithodidae (Crustacea: Decapoda). Sci. Nat. 105, 19.

Kattner, G., Graeve, M., Calcagno, J.A., Lovrich, G.A., Thatje, S., Anger, K., 2003. Lipid, fatty acid and protein utilization during lecithotrophic larval development of *Lithodes santolla* (Molina) and *Paralomis granulosa* (Jacquinot). J. Exp. Mar. Biol. Ecol. 292, 61-74.

Konishi, K., Taishaku, H., 1994. Larval development of *Paralomis hystrix* (De Haan, 1846) (Crustacea, Anomura, Lithodidae) under laboratory conditions. Bull. Nat. Res. Inst. Aquacult. 23, 43-54.

Li, C., von Storch, J.-S., Marotzke, J., 2013. Deep-ocean heat uptake and equilibrium response. Clim. Dynam. 40, 1071-1086.

Lima, F.P., Wethey, D.S., 2012. Three decades of high-resolution coastal sea surface temperatures reveal more than warming. Nat. Comm. 3, 704.

Lovrich, G.A., Thatje, S., Calcagno, J.A., Anger, K., Kaffenberger, A., 2003. Changes in mass and chemical composition during lecithotrophic larval development of the southern king crab, *Lithodes santolla* (Molina). J. Exp. Mar. Biol. Ecol. 288, 65-79.

Marshall, D.J., Krug, P.J., Kupriyanova, E., Byrne, M., Emlet, R.B., 2012. The biogeography of marine invertebrate life histories. Annu. Rev. Ecol. Evol. Syst. 43, 97-114.

Makarov, V.V., 1962. Fauna of the USSR (Crustacea). Israel Program for Scientific Translations, Jerusalem.

McLaughlin, P.A., Anger, K., Kaffenberger, A., Lovrich, G.A., 2001. Megalopal and early juvenile development in *Lithodes santolla* (Molina, 1782) (Decapoda: Anomura: Paguroidea: Lithodidae), with notes on zoeal variations. Invertebr. Reprod. Dev. 40, 53-67.

McLaughlin, P.A., Anger, K., Kaffenberger, A., Lovrich, G.A., 2003. Larval and early juvenile development in *Paralomis granulosa* (Jacquinot) (Decapoda: Anomura: Paguroidea: Lithodidae), with emphasis on abdominal changes in megalopal and crab stages. J. Nat. Hist. 37, 1433-1452.

Morley, S.A., Belchier, M., Dickson, J., Mulvey, T., 2006. Reproductive strategies of sub-Antarctic lithodid crabs vary with habitat depth. Polar Biol. 29, 581-584.

Oliphant, A., Thatje, S., 2013. Per offspring investment implications for crustacean larval development: evolutionary insights into endotrophy and abbreviated development. Mar. Ecol. Prog. Ser. 493, 207-217.

Oliphant, A., Hauton, C., Thatje, S., 2013. The implications of temperature-mediated plasticity in larval instar number for development within a marine invertebrate, the shrimp *Palaemonetes varians*. PLoS ONE 8, e75785.

Paradis, E., 2016. Moran’s autocorrelation coefficient in comparative methods. R vignette.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20, 289-290.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637-669.

Paul, A.J., Paul, J.M., 1999. Development of larvae of the golden king crab *Lithodes aequispinus* (Anomura: Lithodidae) reared at different temperatures. J. Crust. Biol. 19, 42-45.

Paul, A.J., Paul, J.M., 2001. The reproductive cycle of golden king crab *Lithodes aequispinus* (Anomura: Lithodidae). J. Shellfish Res. 20, 369-371.

Pörtner, H.O., Van Dijk, P.L.M., Hardewig, I., Sommer, A., 2000. Levels of metabolic cold adaptation: Tradeoffs in eurythermal and stenothermal ectotherms. In: Davison, W., Howard-Williams, C., Broady, P. (eds) Antarctic Ecosystems: Models for Wider Ecological Understanding. Caxton Press, Christchurch, p 109-122.

Pringle, J.M., Byers, J.E., Pappalardo, P., Wares, J.P., Marshall, D., 2014. Circulation constrains the evolution of larval development modes and life histories in the coastal ocean. Ecology 95, 1022-1032.

Reid, W.D.K., Watts, J., Clarke, S., Belchier, M., Thatje, S., 2007. Egg development, hatching rhythm and moult patterns in *Paralomis spinosissima* (Decapoda: Anomura: Paguroidea: Lithodidae) from South Georgia waters (Southern Ocean). Polar Biol. 30, 1213-1218.

Saborowski, R., Thatje, S., Calcagno, J.A., Lovrich, G.A., Anger, K., 2006. Digestive enzymes in the ontogenetic stages of the southern king crab, *Lithodes santolla*. Mar. Ecol. Prog. Ser. 149, 865-873.

Shirley, T.C., Zhou, S., 1997. Lecithotrophic development of the golden king crab *Lithodes aequispinus* (Anomura: Lithodidae). J. Crust. Biol. 17, 207-216.

Smith, C.C., Fretwell, S.D., 1974. The optimal balance between size and number of offspring. Am. Nat. 108, 499-506.

Smith, K.E., Brown, A., Thatje, S., 2015. The metabolic cost of developing under hydrostatic pressure: experimental evidence supports macroecological pattern. Mar. Ecol. Prog. Ser. 524, 71-82.

Smith, K.E., Aronson, R., Steffel, B.V., Amsler, M.O., Thatje, S., Singh, H., Anderson, J., Brothers, C.J., Brown, A., Ellis, D.S., Havenhand, J.N., James, W.R., Moksnes, P.-O., Randolph, A.W., Sayre-McCord, T., McClintock, J.B., 2017a. Climate change and the threat of novel marine predators in Antarctica. Ecosphere 8, e02017.

Smith, K.E., Aronson, R., Thatje, S., Lovrich, G.A., Amsler, M.O., Steffel, B.V., McClintock, J.B., 2017b. Biology of the king crab *Paralomis birsteini* on the continental slope off the western Antarctic Peninsula. Polar Biol. 40, 2313-2322.

Snow, S., 2010. The evolutionary history and phylogeny of the Lithodidae (Decapoda: Anomura: Lithodidae). PhD thesis, University of Southampton, UK, 275 p.

Strathmann, R.R., 1978. The evolution and loss of feeding larval stages of marine invertebrates. Evolution 32, 894-906.

Thatje, S., 2012. Effects of capability for dispersal on the evolution of diversity in Antarctic benthos. Integr. Comp. Biol. 52, 470-482.

Thatje, S., Hall, S., 2016. The effect of temperature on the evolution of per offspring investment in a globally distributed family of marine invertebrates (Crustacea: Decapoda: Lithodidae). Mar. Biol. 163-48. doi:[10.1007/s00227-015-2776-8](https://doi.org/10.1007/s00227-015-2776-8).

Thatje, S., Mestre, N.C., 2010. Energetic changes throughout lecithotrophic larval development in the deep-sea lithodid crab *Paralomis spinosissima* from the Southern Ocean. J. Exp. Mar. Biol. Ecol. 386, 119-124.

Thatje, S., Calcagno, J.A., Lovrich, G.A., Sartoris, F.J., Anger, K., 2003. Extended hatching periods in the subantarctic lithodid crabs *Lithodes santolla* and *Paralomis granulosa* (Crustacea: Decapoda: Lithodidae). Helgol. Mar. Res. 57, 110-113.

Thatje, S., Anger, K., Calcagno, J.A., Lovrich, G.A., Pörtner, H.-O., Arntz, W.E., 2005. Challenging the cold: crabs reconquer the Antarctic. Ecology 86, 619-625.

Thorson, G., 1936. The larval development, growth, and metabolism of Arctic marine bottom invertebrates compared with those of other seas. Meddelelser om Grøland 100, 1-155.

Van der Have, T.M., De Jong, G., 1996. Adult size in ectotherms: temperature effects on growth and differentiation. J. Theor. Biol. 183, 329-340.

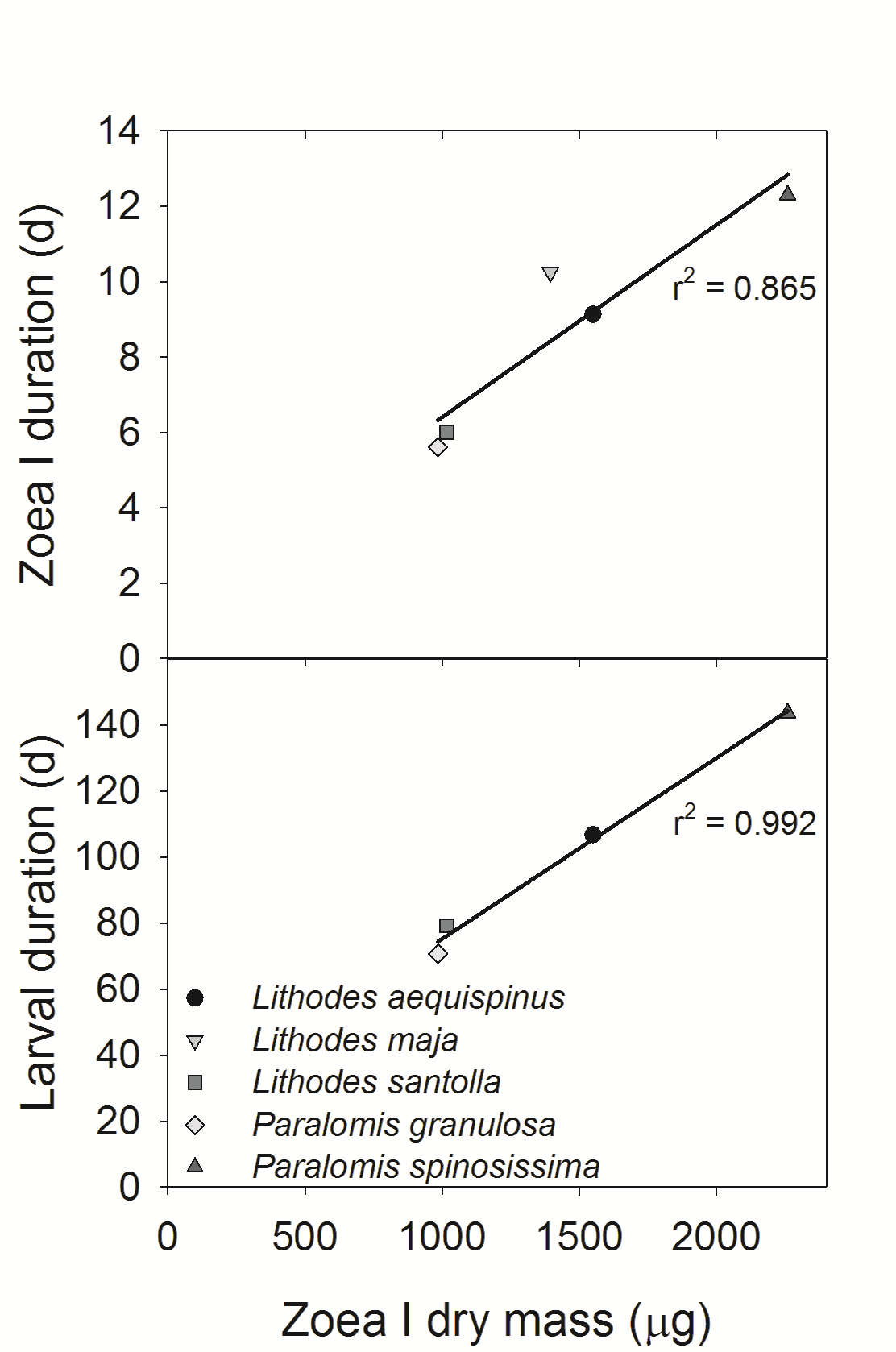
Webb, J., 2014. Reproductive ecology of commercially important lithodid crabs. In: Stevens, B.G. (ed) King crabs of the world Biology and fisheries management. CRC Press, Boca Raton, p 285-314.

White, C.R., Alton, L.A., Frappell, P.B., 2012. Metabolic cold adaptation in fishes occurs at the level of whole animal, mitochondria and enzyme. Proc. Roy. Soc. B 279, 1740-1747.

Zaklan, S.D., 2002a. Evolutionary history and phylogeny of the family Lithodidae. PhD thesis, University of Alberta, Canada, 275 p.

Zaklan, S.D. 2002b. Review of the family Lithodidae (Crustacea: Anomura: Paguroidea): distribution, biology, and fisheries. In: Paul, A.J., Dawe, E.G., Elner, R., Jamieson, G.S., Kruse, G.H., Otto, R.S., Sainte-Marie, B., Shirley, T.C., Woodby, D. (eds) Crabs in Cold Water Regions: Biology, Management, and Economics. Alaska Sea Grant Program, Fairbanks, p 751-845.

**FIGURES AND FIGURE LEGENDSFig. 1** Comparison of dry mass, ratio of carbon to nitrogen contents (C:N), C mass, and N mass of larval stages and juveniles (zoea I = black, zoea II = red, zoea III = green, megalopa = blue, crab I = grey) of deep-water-lineage lithodines reared at 6°C. *Paralomis* spp. have only 2 zoeal stages whereas *Lithodes* spp. have 3 zoea stages. Data are from Brown et al. (2018) for *L*. *maja*, Lovrich et al. (2003) for *L*. *santolla*, and Calcagno et al. (2003) for *P*. *granulosa*.



**Fig. 2** Correlation between zoea I dry mass and zoea I duration or larval duration of lithodine crabs from deep-water lineages at 5°C. Data are from Shirley and Zhou (1997) and Paul and Paul (1999) for *Lithodes aequispinus*, Brown et al. (2018) for *L*. *maja*, Lovrich et al. (2003) and Anger et al. (2004) for *L*. *santolla*, Calcagno et al. (2003) and Anger et al. (2003) for *Paralomis granulosa*, and Thatje and Mestre (2010) for *P. spinosissima*.

**TABLES**

**Table 1** Fitted parameters (a, b) and coefficients of determination (r2) of non-linear power regression equations (D = a × Tb) 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 | r2 | Source |
| Zoea I | *Lithodes aequispinus* | 26.4 | -0.660 | 1.000 | Paul and Paul 1999 |
|  | *Lithodes maja* | 37.8 | -0.811 | 0.988 | Brown et al. 2018 |
|  | *Lithodes santolla* | 17.9 | -0.679 | 0.971 | Anger et al. 2004 |
|  | *Paralomis granulosa* | 16.9 | -0.685 | 0.997 | Anger et al. 2003 |
| Larval | *Lithodes aequispinus* | 299.5 | -0.641 | 0.994 | Paul and Paul 1999 |
|  | *Lithodes santolla* | 450.6 | -1.080 | 0.995 | Anger et al. 2004 |
|  | *Paralomis granulosa* | 349.8 | -0.993 | 0.995 | Anger et al. 2003 |