

When is warmer better? Disentangling within- and between-generation effects of thermal history on early survival

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Abstract

1. Understanding the fitness consequences of thermal history is necessary to predict organismal responses to global warming. This is especially challenging for ectotherms with complex life cycles, where distinct life stages can differ in thermal sensitivity, acclimate to different thermal environments and accrue responses to acclimation within and between generations.
2. Although acclimation is often hypothesized to benefit organisms by helping them (or their offspring) to compensate for negative impacts of environmental change, mixed support for this hypothesis highlights the need to assess alternatives. Assessments that explicitly dissect responses across life stages and generations, however, remain limited.
3. We assess alternative hypotheses of acclimation (none, beneficial, colder-is-better and warmer-is-better) within and between generations of a marine tubeworm whose vulnerability to warming rests on survival at early planktonic stages (gametes, embryos and larvae). First, we acclimate parents, gametes and embryos to ambient and projected warmer temperatures (17°C and 22°C) factorially by life stage. Next, we rear offspring with differing acclimation histories to the end of larval development at test temperatures from 10°C to 28°C (lower and upper survival limits respectively). Last, we estimate thermal survival curves for development, and compare them among thermal histories.
4. We show that survival curves are most responsive to parental acclimation followed by acclimation at embryogenesis, but are buffered against acclimation at fertilization. Moreover, curves respond independently to acclimation within and between generations, and respond largely as predicted by the warmer-is-better hypothesis, despite the semblance of beneficial acclimation after successive doses of warmer temperature.
5. Our study demonstrates the varied nature of thermal acclimation and the importance of considering how responses aggregate across complex life cycles when predicting vulnerability to warming.

KEYWORDS

acclimation, complex life cycles, early life stages, embryo development, larval development, parental effects, thermal performance

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1 | INTRODUCTION

Global warming is affecting biological function from molecules to ecosystems, with key implications for many ectotherms that do not, or cannot, thermoregulate (Clarke, 2017; Deutsch et al., 2008; Seebacher et al., 2015). Their capacity to survive and reproduce in the face of warming rests on thermally sensitive life stages acting as life cycle bottlenecks (Dahlke et al., 2020; Sunday, 2020). It also rests on the extent to which thermal history (the temperatures experienced by prior generations or life stages) buffers those stages against warming or worsens its impacts (Donelson et al., 2018; Kellermann et al., 2017). Recent work points to greater thermal sensitivity at early life stages relative to juveniles and adults (Dahlke et al., 2020; Kingsolver & Buckley, 2020; Pandori & Sorte, 2019), yet the role of thermal history remains unclear. Despite the documented effects of thermal history on thermal sensitivity within and between generations (e.g. Crill et al., 1996; Diaz et al., 2021; Huey et al., 1995; Le Roy & Seebacher, 2018; Steigenga & Fischer, 2007), there is a need to explicitly dissect those effects across the complex life cycles of ectotherms, especially at life stages most vulnerable to warming.

Acclimation to thermal stress has long been thought to enhance the fitness of organisms who reencounter that stress later in life, giving them an adaptive advantage over nonacclimated organisms (Hochachka & Somero, 1984; Hoffmann & Parsons, 1991; Levins, 1969). This so-called beneficial acclimation hypothesis (Leroi et al., 1994) has been framed more broadly in terms of adaptive phenotypic plasticity to other environmental stressors (Ghalambor et al., 2007; Via et al., 1995). It has also been extended to parental acclimation, positing that parental exposure to stress primes offspring to tolerate that stress better than offspring from nonstressed parents (Agrawal et al., 1999; Donelson et al., 2012). Despite various textbook examples, however, literature surveys now challenge the beneficial acclimation hypothesis in its various forms. Regardless of whether responses are surveyed within generations (Angilletta, 2009; Sgrò et al., 2016; Woods & Harrison, 2002) or across them (Donelson et al., 2018; Sánchez-Tójar et al., 2020; Sgrò et al., 2016; Uller et al., 2013), acclimation is just as often neutral to fitness, or even detrimental in more stressful environments (Sánchez-Tójar et al., 2020). Such mixed responses to acclimation highlight the need to consider alternative hypotheses and predictions.

Multiple hypotheses predict how acclimation to stressfully warmer temperatures may affect thermal performance curves, which describe fitness at different test temperatures (Figure 1; Huey & Berrigan, 1996; Huey et al., 1999). If the beneficial acclimation hypothesis holds, then acclimation should compensate for heat stress by increasing the thermal optimum at no cost to fitness (Figure 1a). Conversely, if acclimation is detrimental (e.g. compensation is outweighed by costs of physiological damage or smaller body size), then nonacclimated organisms should outperform acclimated ones at each test temperature (Figure 1b). However, if

acclimation has thermodynamic effects that improve physiological activity (Angilletta et al., 2010; Huey & Kingsolver, 1989), then acclimated organisms should have a higher maximum and thermal optimum than nonacclimated ones (Figure 1c). No effect of acclimation (Figure 1d) may reflect developmental mechanisms that buffer fitness against perturbation (Huey et al., 1999). Acclimation may, of course, have more nuanced effects, and be increasingly detrimental as thermal limits are met. Nevertheless, in the absence of thermodynamic effects, selection should drive thermal optima towards the mean environmental temperature (Asbury & Angilletta, 2010). Characterizing acclimation to projected changes in mean temperature using the framework above may thus shed light on responses to warming (Einum et al., 2019; Sinclair et al., 2016). Efforts to do so lend weight to the warmer-is-better hypothesis (Huey et al., 1999; Treasure & Chown, 2019; see also Einum et al., 2019), but rarely explore responses between generations except in microbes.

Uncertainty surrounds the relative strengths of responses to acclimation within versus between generations and how responses aggregate across complex life cycles (Donelson et al., 2018; Sgrò et al., 2016; Williams et al., 2016). Theory often predicts shifts in thermal optima and/or breadths depending on how well temperature cues at one life stage predict selection at another stage (Angilletta, 2009), and whether responses aggregate over time through effects on survival or reproduction (Gabriel & Lynch, 1992; Gilchrist, 1995). Limited support for such predictions, however, suggests that unpredictable cues might produce other responses such as bet-hedging (Buckley & Kingsolver, 2021; Seebacher & Little, 2021), or responses at different stages might combine in unanticipated ways as they aggregate over time (Angilletta, 2009; Loeschcke & Hoffmann, 2002). Ultimately, studies are needed that not only test alternative hypotheses of acclimation, but also disentangle responses within and between generations. To date, such studies are rare (Crill et al., 1996; Huey et al., 1995; Le Roy & Seebacher, 2018), and support neither clear trends in the strengths of responses at different stages, nor particular hypotheses when responses are considered in aggregate.

Here, we assess alternative hypotheses of acclimation, and disentangle responses within and between generations, in the externally fertilizing tubeworm, *Galeolaria caespitosa*. Like most aquatic ectotherms, its vulnerability to warming rests on survival at early planktonic stages (gametes, embryos and larvae) that disperse passively for days to weeks in currents (Byrne et al., 2020; Dahlke et al., 2020; Walsh et al., 2019). This couples survival in early life to water temperature, while decoupling the temperature experienced in early life from parental temperature (Lotterhos et al., 2021). Nevertheless, parents can still modify offspring responses to temperature by loading cellular defences into gametes, or transmitting physiological damage sustained in their own lifetimes (Chirgwin et al., 2018; Guillaume et al., 2016; Hamdoun & Epel, 2007). Temperatures at fertilization and embryogenesis can likewise modify responses to temperature later in life (Chirgwin et al., 2021; Rebollo et al., 2021).

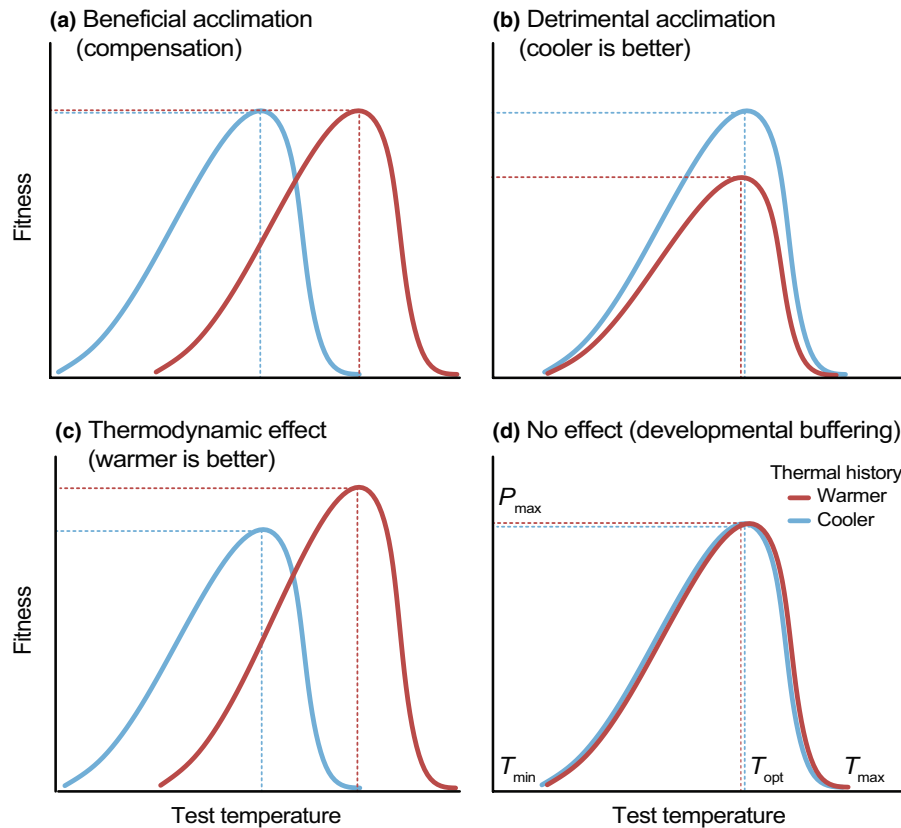


FIGURE 1 (a–d) Hypotheses of acclimation to heat stress and their predictions for thermal performance of acclimated (red) versus nonacclimated (blue) organisms. Fitness is a unimodal function of test temperature, rising from zero at its lower thermal limit (T_{\min}) to a maximum (P_{\max}) at its thermal optimum (T_{opt}), then returning to zero at its upper thermal limit (T_{\max}). (a) If the beneficial acclimation hypothesis holds, then acclimation should compensate for heat stress by increasing the thermal optimum at no cost to fitness. (b) If acclimation is detrimental (i.e. cooler is better), then nonacclimated organisms should outperform acclimated ones at each test temperature. (c) If acclimation has thermodynamic effects that enhance physiological activity (i.e. warmer is better), then acclimated organisms should have a higher maximum and thermal optimum than nonacclimated ones. (d) No effect of acclimation may reflect developmental buffering of fitness against perturbation. Hypotheses adapted from Huey et al. (1999).

This biology therefore presents rare scope to dissect cumulative responses to acclimation across key stages of the life cycle that govern adult abundances and dynamics.

Using a split-cohort design to standardize genetic backgrounds across life stages, we first acclimate parents, gametes and embryos to ambient and stressfully warmer mean temperatures (17°C and 22°C) factorially by stage. Next, we rear offspring with differing acclimation histories to the end of larval development at eight test temperatures from 10°C to 28°C (lower and upper survival limits respectively). Last, we estimate thermal survival curves for development, and compare curves to hypotheses in Figure 1. Specifically, we predict that acclimation to heat stress will increase the thermal optimum if the beneficial acclimation hypothesis holds (Figure 1a), reduce survival if the cooler-is-better hypothesis holds (Figure 1b), increase the thermal optimum and maximum if the warmer-is-better hypothesis holds (Figure 1c), or have no effect if offspring are buffered against stress as they develop (Figure 1d). By factorially manipulating thermal history, we further dissect acclimation responses within and between generations to explore how they aggregate across the life cycle.

2 | MATERIALS AND METHODS

2.1 | Study species and sampling

Galeolaria caespitosa (henceforth *Galeolaria*) is an ecosystem engineer of rocky shores across temperate Australia, forming dense colonies of tubes used as habitat and refuge by associated communities (Wright & Gribben, 2017). Sessile adults breed year-round by releasing gametes into the sea for external fertilization (Chirgwin et al., 2020). Embryos develop into independent larvae ~24h, then larvae develop for another ~2–3 weeks until rapid changes in size, morphology and behaviour signal the end of planktonic life (readiness to settle and recruit to sessile populations; Marsden & Anderson, 1981). These early stages are thermal bottlenecks in the life cycle (Byrne, 2011; Dahlke et al., 2020; Walsh et al., 2019), but the aggregate effects of thermal history on survival across them are unknown.

We sampled cohorts of parents between June and December 2020 from a natural population at Brighton, Victoria, where annual mean water temperature is ~17°C (Chirgwin et al., 2017). The region

is warming much faster than the global mean (Hobday & Pecl, 2014), is projected to warm $\sim 2\text{--}4^\circ\text{C}$ by the century's end (RCP8.5 relative to 1980–1999; Lough et al., 2012), and is prone to heatwaves above mean warming (Oliver et al., 2017). Each cohort was transferred in seawater to Monash University, held for several hours at the natural temperature to minimize transfer stress, then divided among replicate tanks of fresh aerated seawater and gradually adjusted to the designated parental temperature (see below). Collection of *Galeolaria* was conducted under the Victorian Fisheries Authority permit number RP1328.

2.2 | Experimental overview

We factorially manipulated parental temperature (17°C vs. 22°C), temperature at fertilization (17°C vs. 22°C) and temperature at embryogenesis (17°C vs. 22°C), then estimated thermal survival curves for larval development (Figure 2). Prior acclimation temperatures approximated the annual mean and $\sim 2^\circ\text{C}$ above the summer mean in nature (Chirgwin et al., 2017; Lough et al., 2012), and spanned thermal optima for fertilization and embryogenesis (Rebolledo et al., 2020). Survival was assayed at eight test temperatures spanning lower and upper limits ($10\text{--}28^\circ\text{C}$) for larval development (Rebolledo et al., 2020).

Except for parents, we manipulated temperature and assayed survival (of 30 offspring per assay) in replicate vials of filtered,

pasteurized seawater. Vials were loosely capped for oxygen flow and suspended upright in water baths held at designated temperatures ($\pm 0.1^\circ\text{C}$) by immersion heaters (Grant Optima TX150). For each cohort of parents, replicates were generated in an incomplete block design with test temperatures assigned haphazardly to blocks. Each block comprised three replicates per combination of acclimation temperatures, assayed at five to eight test temperatures (it was not logistically feasible to assay all eight test temperatures per block). All replicates per block had the same cohort of parents and were assayed for survival concurrently under identical conditions aside from the manipulation of temperature (Figure 2). This design was then replicated for each of four cohorts of parents. In total, survival was scored for $\sim 17,000$ offspring in 574 vials (2 parental temperatures \times 2 fertilization temperatures \times 2 temperatures at embryogenesis \times ~ 6 test temperatures on average \times 4 blocks \times 3 replicates per block, minus 2 replicates lost due to contamination).

2.3 | Manipulation of parental temperature

Since reproduction is continuous and gametes can ripen in under 2 weeks (Chirgwin et al., 2018), parents were acclimated at either 17°C or 22°C for 1 month prior to the steps below. Each cohort of parents was acclimated in replicate tanks per temperature, fed a mix of live microalgae ad libitum every second day, and had seawater replaced weekly.

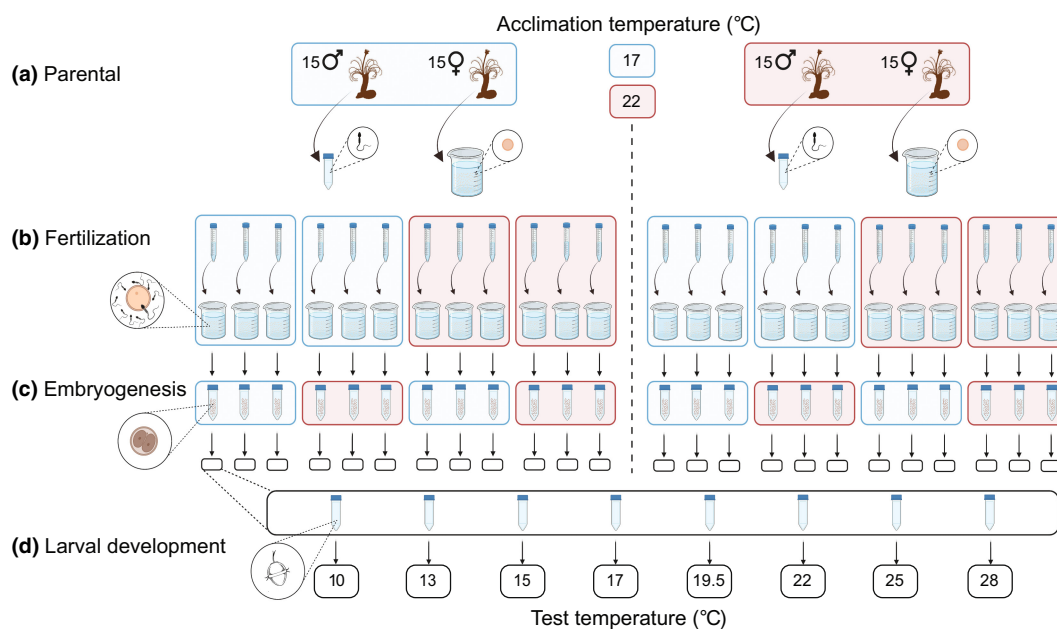


FIGURE 2 Factorial manipulation of thermal history. (a) Parents were acclimated at either 17°C or 22°C for 1 month, then gametes from 15 males and 15 females per temperature were pooled by sex. (b) Fertilizations were initiated at 17°C and 22°C , so that fertilization and parental temperatures were crossed factorially in six replicate vials per combination. After 30 min, vial contents were rinsed of sperm and incubated at the same temperature until two-cell embryos formed 1–2 h later. (c) Embryos from each vial were transferred to either 17°C or 22°C , so that temperatures at this stage and prior stages were crossed factorially in three replicate vials per combination, until larvae formed ~ 24 h later. (d) Larvae from each vial were transferred to each of five to eight test temperatures, so that temperatures at this stage and prior stages were again crossed factorially in three replicate vials per combination. Larvae were monitored until they either died or successfully completed development up to 3 weeks later. The design was replicated for four cohorts of parents. Figure created with Biorender.

2.4 | Gamete collection and manipulation of temperature at fertilization

For each cohort of acclimated parents, gametes were collected from 15 males and 15 females per parental temperature (to minimize the effects of genetic incompatibilities; Chirgwin et al., 2017). Sexes came from different tanks to minimize tank effects. Each adult was extracted from its tube and placed in ~1 mL of fresh filtered seawater at 17°C to spawn. Gametes were checked for quality based on appearance of eggs and motility of sperm, then pooled by sex and used within the hour before viability declines (Rebolledo et al., 2020). Pooled eggs were diluted to ~250 cells mL⁻¹ before use. Pooled sperm were kept concentrated at ~10⁷ cells mL⁻¹ to minimize activity-dependent aging before use (Chirgwin et al., 2020; Kupriyanova, 2006).

Gametes from each parental temperature were used to initiate replicate fertilizations at 17 and 22°C, so that fertilization and parental temperatures were crossed factorially in six replicate vials per combination (Figure 2). For each fertilization, 4.5 mL of pooled eggs and 0.5 mL of pooled sperm were adjusted separately to the required temperature over 30 min, then combined at that temperature. After 30 min of contact (which maximizes fertilization success across the temperatures here; Rebolledo et al., 2020), the contents of each vial were rinsed through 0.25 µm mesh to remove sperm, then incubated in 45 mL of fresh seawater at the same temperature. Zygotes divided to form embryos ~1–2 h later, which is the earliest they are reliably distinguished from unfertilized eggs under a stereomicroscope.

2.5 | Manipulation of temperature at embryogenesis

Embryos from each vial were transferred to new vials at either 17°C or 22°C, so that temperatures at this stage and prior stages were crossed factorially in three replicate vials per combination (Figure 2). All embryos were at a similar point in development (two cells) when transferred. Embryos were incubated in 45 mL of seawater, sufficient to avoid oxygen limitation (Chirgwin et al., 2018), until they completed development into swimming, feeding larvae up to ~24 h later.

2.6 | Assaying survival of larval development

Thirty larvae per vial were transferred randomly to each of three to four replicate vials per test temperature (10, 13, 15, 17, 19.5, 22, 25 or 28°C), so that temperatures at this stage and prior stages were again crossed factorially (Figure 2). Larvae were incubated in 10 mL of seawater, sufficient to avoid oxygen limitation (Chirgwin et al., 2018), and fed a mix of nonlive microalgae ad libitum (~1 × 10⁴ cells mL⁻¹ every second day), with seawater partially replaced at this point. We used nonlive microalgae to avoid confounding effects of food availability if live microalgae grew at different rates at different

temperatures. After a week, all but one of the vials per test temperature were sampled daily to check developmental progression (which is incomplete before this time; Rebolledo et al., 2020). The remaining vial was undisturbed. Sampling ended when all larvae in sampled vials either died or successfully completed development, up to 3 weeks later depending on temperature. Survival was then assayed in the undisturbed vial. No data from other vials entered analyses.

2.7 | Modelling thermal survival curves

We fitted thermal survival curves to binary data (scores of 1 if offspring survived development and 0 otherwise) using a binomial mixed-effects regression model fitted with a logit link and Laplace approximation in the LME4 package (version 1.1-26; Bates et al., 2015) for R v4.0.5 (R Core Team, 2021). Based on unconstrained smoothers fitted to data, survival curves were modelled as cubic functions of test temperature using orthogonal polynomials. Acclimation temperatures and all possible interactions with curves were initially included as fixed effects, before three- and four-way interactions were excluded to avoid overfitting (this did not reduce model fit; Table 1). Block was also included as a fixed effect, as was vial as a random effect to avoid pseudoreplication (Bolker et al., 2009; Harrison et al., 2018). Our mixed-effects model is preferable to analysing vial-level counts of individual successes and failures, which assumes that individuals within vials are independent and have equal probability of success (Zuur et al., 2009). It also preferable to analysing vial-level proportions, which causes distributional problems and ignores within-vial counts unless weighted by them (vial-level approaches are then equivalent; Zuur et al., 2009). Checks of model assumptions using the DHARMa package (version 0.4.1; Hartig, 2021) showed no violations. Fixed effects were tested using Wald χ^2 tests (Bolker et al., 2009) in the CAR package (version 3.0-10; Fox & Weisberg, 2019). Pairwise contrasts were done for significant effects using z tests of log odds ratios (Sidak-adjusted as necessary) in the EMMEANS package (version 1.6.0; Lenth et al., 2021).

2.8 | Estimates and confidence intervals of curve descriptors

For acclimation temperatures with significant effects on survival curves, we extracted curve descriptors from the fitted model. Thermal optimum (T_{opt}) was calculated as the temperature of maximal survival (P_{max}), and thermal limits (T_{min} and T_{max}) were calculated as the lower and upper temperatures at which survival was 5% of its maximum. We used 5% because binary data may approach 0% via an asymptote, making T_{min} and T_{max} less meaningful at complete mortality (Kellermann et al., 2019), and limits were qualitatively unchanged when calculated at complete mortality. Thermal tolerance ($T_{max} - T_{min}$) and thermal breadth (calculated as the temperature range at which survival was at least 50% of its maximum; Sinclair et al., 2016) were also explored, but are omitted here because they did not add to the conclusions drawn from other descriptors.

TABLE 1 Effects of parental temperature, temperature at fertilization and temperature at embryogenesis on the probability of surviving larval development. Survival was modelled as a cubic function of test temperature in a binomial mixed-effects regression. Higher-order interactions were nonsignificant (joint χ^2 test = 2.06, $df = 13$, $p = 0.99$) and were removed from the model to avoid overfitting.

Fixed effects	χ^2	df	<i>p</i>
Parental temperature	7.36	1	<0.01
Temperature at fertilization	0.30	1	0.58
Temperature at embryogenesis	0.00	1	0.96
Test temperature for larvae (linear, quadratic and cubic trends)	4970.21	3	<0.001
Parental temperature × temperature at fertilization	0.14	1	0.70
Parental temperature × temperature at embryogenesis	3.89	1	0.05
Temperature at fertilization × temperature at embryogenesis	0.01	1	0.94
Parental temperature × test temperature	120.20	3	<0.001
Temperature at fertilization × test temperature for larvae	1.97	3	0.58
Temperature at embryogenesis × test temperature for larvae	31.25	3	<0.001
Block	35.50	3	<0.001

p-values in bold are significant at $\alpha = 0.05$.

To compare descriptors between acclimation temperatures and evaluate hypotheses in Figure 1, we estimated the mean and 95% confidence interval of each descriptor from 1000 parametric bootstrap samples gained by permuting the fitted model in the `BOOT` package (v1.3-27; Cauty & Ripley, 2021). Descriptors were considered to differ significantly between temperatures if their 95% confidence intervals did not overlap. Because this may be only a rough guide to significance, we also calculated formal contrasts of means between temperatures (where means differ if the 95% confidence interval of their contrast excludes 0). Both methods gave similar results, so we rely on the former for ease of visualization.

3 | RESULTS

3.1 | Modelling thermal survival curves

Parental temperature and temperature at embryogenesis had interactive effects on mean survival regardless of test temperature (Table 1 and Figure 3), but independent effects on thermal survival curves—that is, mean survival at different test temperatures (Table 1 and Figure 4). Temperature at fertilization did not affect mean survival, alone or in combination with any other temperature (Table 1).

Based on pairwise contrasts, acclimation temperatures had interactive effects on mean survival because parental acclimation

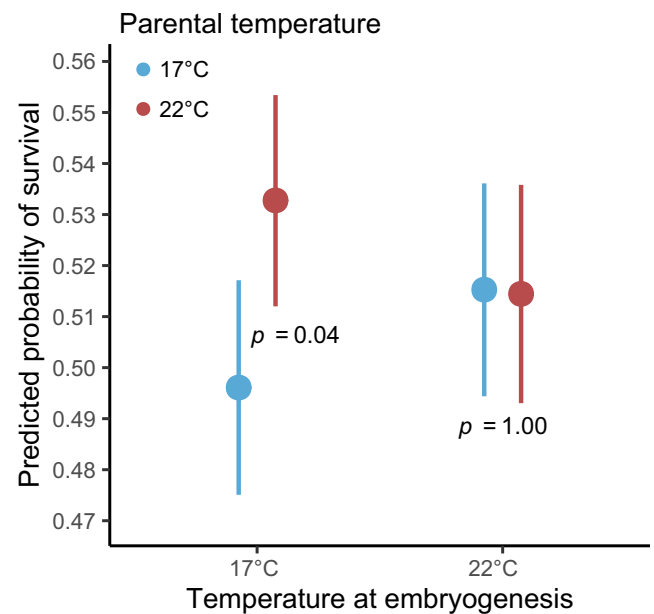


FIGURE 3 Interactive effects of parental temperature and temperature at embryogenesis on the predicted probability of surviving larval development, regardless of test temperature. Solid points are means ($\pm 95\%$ confidence intervals). Parental acclimation at 22°C improved survival when followed by embryogenesis at 17°C but not when followed by embryogenesis at 22°C. Survival was unaffected by temperature at fertilization.

at 22°C increased the probability of survival when embryogenesis occurred at 17°C ($z = |2.54|$, $p = 0.04$), but not when it occurred at 22°C ($z = |0.06|$, $p = 1.00$; Figure 3). Acclimation temperatures had independent effects on thermal survival curves because linear trends (average slopes of curves in Figure 4) were consistently positive (Figure 5a), but significantly more so after parental acclimation at 22°C ($z = |9.53|$, $p < 0.01$) and embryogenesis at 22°C ($z = |5.01|$, $p < 0.01$). Likewise, cubic trends (initial slopes of curves in Figure 4) were consistently negative (Figure 5c), but significantly more so after parental acclimation at 22°C ($z = |6.16|$, $p < 0.01$; Figure 5c) and embryogenesis at 22°C ($z = |3.31|$, $p < 0.01$). Quadratic trends (breadths of curves in Figure 4) were unresponsive to either acclimation temperature (Figure 5b).

3.2 | Estimates and confidence intervals of curve descriptors

As suggested by trends above, maximal survival and the thermal optimum for survival responded more to parental temperature than to temperature at embryogenesis (Figure 6a,b). Thermal limits for survival were unresponsive to either temperature (Figure 6c,d), as were thermal tolerance and thermal breadth (not presented).

Independent of temperature at embryogenesis, the maximal survival of larvae was significantly higher when parents acclimated at 22°C than when they acclimated at 17°C (Figure 6a). Consistent with the warmer-is-better hypothesis (Figure 1c), this increase in maximal

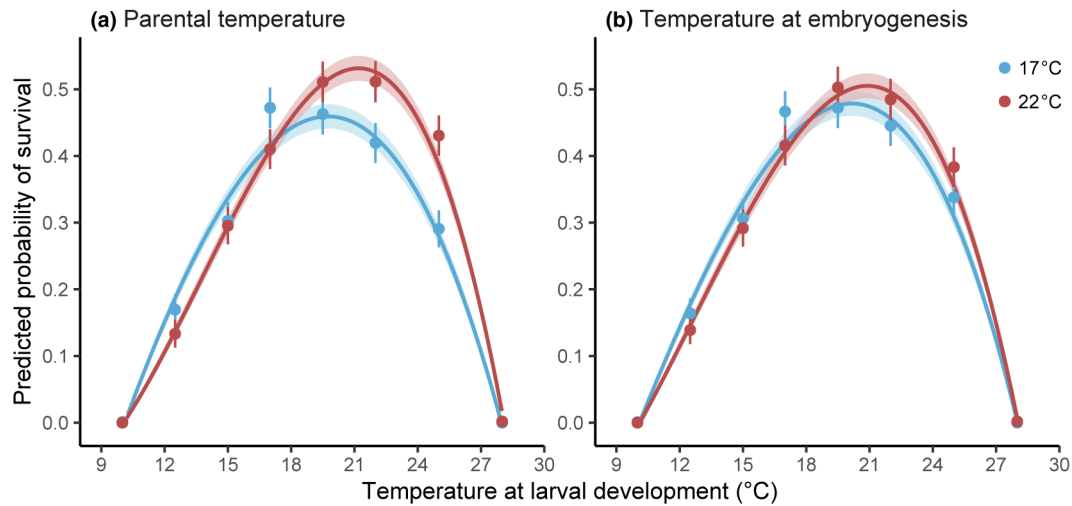


FIGURE 4 Independent effects of (a) parental temperature and (b) temperature at embryogenesis on the predicted probability of surviving larval development at different test temperatures. Survival curves for parental temperatures are averaged across temperatures at embryogenesis, and vice versa. Shaded areas are 95% confidence intervals of curve predictions. Points are observed proportions (\pm 95% confidence intervals) of survival at each test temperature. Survival was unaffected by temperature at fertilization.

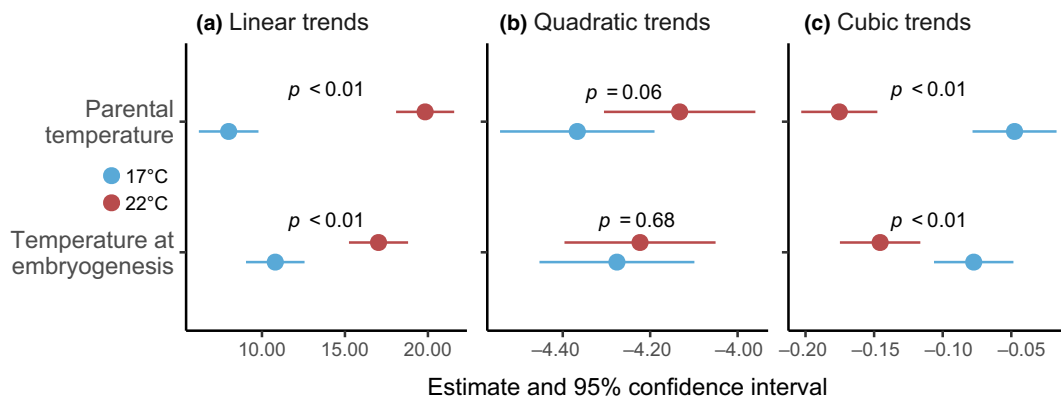


FIGURE 5 Independent effects of parental temperature and temperature at embryogenesis on (a) linear, (b) quadratic and (c) cubic trends estimated for survival curves in Figure 4. Trends describe curves' average slopes, breadths and initial slopes respectively. Trends for parental temperatures are averaged across temperatures at embryogenesis, and vice versa. Estimates (points) and 95% confidence intervals (bars) all exclude zero and are multiplied by 100 to aid visualization of different scales. Survival was unaffected by temperature at fertilization.

survival coincided with a significant increase in the thermal optimum for survival, which was 1.2°C higher when parents acclimated at 22°C than when they acclimated at 17°C (Figure 6b).

Independent of parental temperature, warmer temperature at embryogenesis also increased the thermal optimum for survival, which was 0.6°C higher when embryos developed at 22°C than when they developed at 17°C (Figure 6b). This increase in optimum coincided with only a small, nonsignificant increase in maximum (Figure 6a), making it inseparable statistically from predictions of the beneficial acclimation hypothesis (Figure 1a).

4 | DISCUSSION

Understanding the fitness consequences of thermal history is necessary to predict organismal responses to global warming,

especially for ectotherms with distinct life stages that can differ in thermal sensitivity, acclimate to different thermal environments and accrue responses within and between generations (Donelson et al., 2018; Kellermann et al., 2017; Williams et al., 2016). Here in *Galeolaria*, an aquatic ectotherm whose early planktonic stages (gametes, embryos and larvae) are especially vulnerable to warming (Byrne et al., 2020; Dahlke et al., 2020; Walsh et al., 2019), we show that thermal survival curves are most responsive to parental acclimation followed by acclimation at embryogenesis, but are buffered against acclimation at fertilization. Moreover, curves respond independently to acclimation within and between generations, and respond largely as predicted by the warmer-is-better hypothesis, despite converging on the predictions of the beneficial acclimation hypothesis after successive acclimations to warmer temperature. Our results demonstrate the varied nature of thermal acclimation, and the importance of considering how acclimation responses

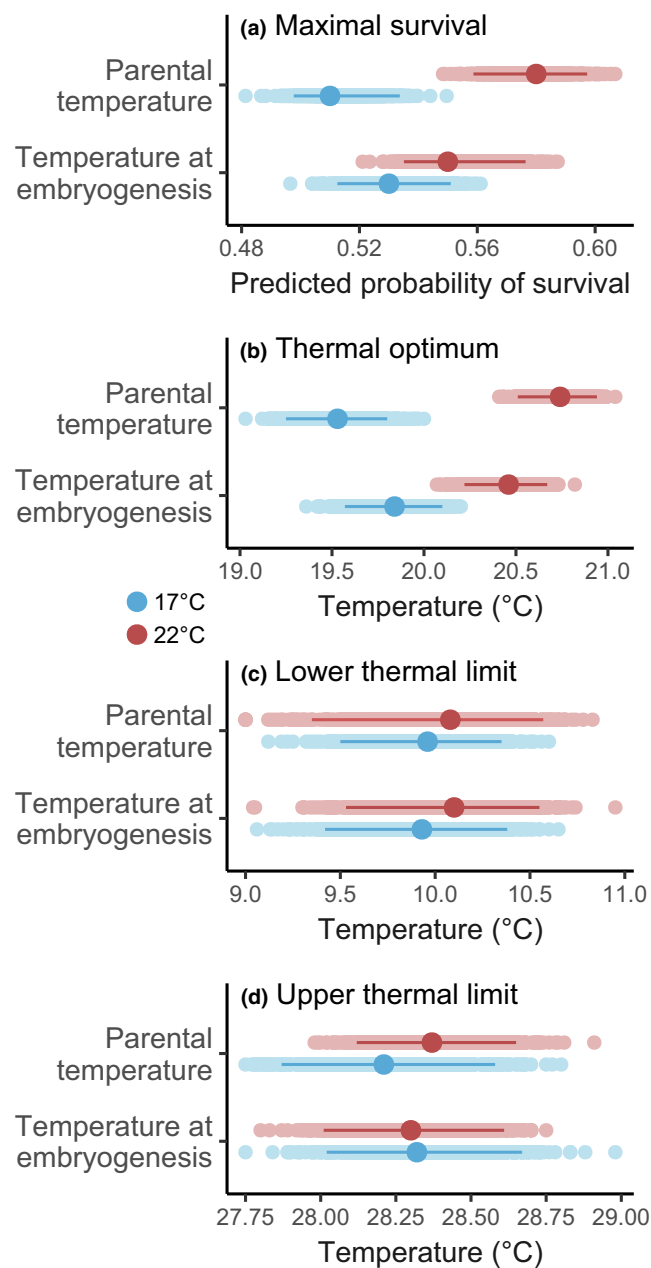


FIGURE 6 Effects of parental temperature and temperature at embryogenesis on descriptors of survival curves in [Figure 4](#): (a) maximal survival, (b) thermal optimum and (c, d) thermal limits. Descriptors for parental temperatures are averaged across temperatures at embryogenesis, and vice versa. Estimates (solid points) and 95% confidence intervals (bars) are from 1000 bootstrap replicates (transparent points) of the model used to fit curves. Survival was unaffected by temperature at fertilization.

accumulate across complex life cycles when predicting the impacts of warming.

Drawing on thermodynamic principles, the warmer-is-better hypothesis argues that warmer temperatures confer greater bioenergetic capacity than cooler temperatures, and so organisms with higher thermal optima should have higher maximal fitness than organisms with lower optima (Buckley & Kingsolver, 2021; Sørensen et al., 2018; Treasure & Chown, 2019). To our knowledge, responses

to parental acclimation in line with this hypothesis have not yet been documented, despite much scrutiny of parental effects and debate over their adaptive value (Donelson et al., 2018; Sánchez-Tójar et al., 2020; Uller et al., 2013). This could reflect the long tradition of testing acclimation by assessing offspring fitness in two test environments either matched or mismatched to two parental environments (the 2×2 designs synthesized in Seebacher et al., 2015; Uller et al., 2013), which gives limited scope to distinguish between the warmer-is-better and beneficial acclimation hypotheses. Mechanisms underlying the transfer of acclimation effects from parents to offspring remain contentious (McGuigan et al., 2021), but may include the loading of cellular defences such as stress-response proteins into developing gametes before fertilization (Burton & Metcalfe, 2014; Gulyas & Powell, 2019; Lockwood et al., 2017). Such defences are upregulated at warmer temperatures, give front-line protection against thermal stress, and may not be synthesized by mature gametes or early embryos (Feder & Hofmann, 1999; Hamdoun & Epel, 2007; Sørensen et al., 2003). They therefore offer a plausible pathway for parental acclimation to induce warmer-is-better effects in offspring, and could also buffer offspring against acclimation at fertilization given its lack of effect in our study (consistent with [Figure 1d](#)).

Acclimation of embryos had more ambiguous effects on survival curves. Statistically, at least, larvae compensated for warmer temperature at embryogenesis by increasing their thermal optimum at no cost to maximal survival, as predicted by the beneficial acclimation hypothesis ([Figure 1a](#); Leroi et al., 1994; Sørensen et al., 2018). Given, however, that the increase in optimum was weaker than that induced by parental acclimation, and coincided with a weak (nonsignificant) increase in maximum, responses to acclimation at this life stage were still in the direction of the warmer-is-better hypothesis. This could again point to the involvement of stress-response proteins, which are often unexpressed early in embryogenesis when they can inhibit cell division and signalling (Feder & Hofmann, 1999; Hamdoun & Epel, 2007). Planktonic embryos are instead thought to evolve faster development at stages with less protection against stress (Strathmann et al., 2002). A shortened window of exposure, and nonexpression of cellular defences for part of it, might then give embryos limited capacity to respond to acclimation. Alternatively, cumulative damage from successive doses of heat stress might counter gains in fitness from parental acclimation (Buckley & Kingsolver, 2021; Williams et al., 2016). That larvae survived better when parental acclimation at 22°C was followed by embryogenesis at 17°C, but not embryogenesis at 22°C ([Figure 3](#)), supports this idea. If so, responses matching the beneficial acclimation hypothesis could emerge not only from adaptation, but also the interplay of damage and thermodynamic effects across the life cycle.

The relative strengths of responses to acclimation within versus between generations in *Galeolaria* go against meta-analyses finding that parental environmental effects often fail to buffer offspring fitness against stress (Sánchez-Tójar et al., 2020; Uller et al., 2013).

One reason may be that such analyses synthesize diverse environmental factors with mixed effect sizes, yet targeted reviews of responses to parental temperature find similar results (Donelson et al., 2018; Sgrò et al., 2016). Another reason may be that the life history characteristics of aquatic ectotherms, combined with higher thermal inertia (and hence predictability) in water than on land, offer more scope for mechanisms of temperature compensation to evolve (Sørensen et al., 2018). In external fertilizers like *Galeolaria*, for example, high mortality at early life stages that disperse passively in currents leads to strong coupling of physical and evolutionary processes, while decoupling the environments of early stages and adults (Lotterhos et al., 2021). In such cases, temperature may vary more between generations than within them for the stages considered here, favouring stronger responses to parental acclimation than to acclimation in early development (Angilletta, 2009; Le Roy & Seebacher, 2018). While further tests are needed, a recent review citing benefits of transgenerational acclimation in 47% of studies on aquatic invertebrates compared to 26% of studies on terrestrial ones gives qualified support for this idea (Donelson et al., 2018; see also Byrne et al., 2020).

To our knowledge, our study remains one of only a few to explore alternative hypotheses of acclimation, and explicitly dissect responses within and between generations (Huey et al., 1995; Zamudio et al., 1995; see also Le Roy & Seebacher, 2018). More often, as noted above, parental acclimation temperatures are crossed with offspring test temperatures in ways that neither distinguish among competing hypotheses of acclimation, nor assess cumulative responses to it. Consequently, we lack a clear picture of how such responses aggregate within generations and from one generation to the next (Buckley & Kingsolver, 2021; Williams et al., 2016). In other work on *Galeolaria*, for instance, larval survival at warmer temperature was increased by parental acclimation (Chirgwin et al., 2018), but decreased by acclimation of gametes (Chirgwin et al., 2021), while acclimation of embryos increased the thermal optimum for survival by $\sim 2^{\circ}\text{C}$ (Rebolledo et al., 2021). However, temperatures of embryos and larvae were conflated in the first two studies, and parents were unacclimated in the second two. Our results here thus caution against interpreting responses to acclimation at different life stages, and using them to predict vulnerability to warming, without considering them in aggregate.

Overall, thermal acclimation in *Galeolaria* differs within and between generations in ways that support the potential transfer of thermodynamic (warmer-is-better) effects from parents to offspring. Acclimation of parents and, to lesser extent, embryos increased not only the thermal optimum for larval survival, but also the chance of survival at that new optimum, without compromising thermal limits or breadth. It is unclear, though, how well acclimation responses like this can buffer vulnerable planktonic stages from projected warming of $\sim 2\text{--}4^{\circ}\text{C}$ (relative to 1980–1999) by the century's end (Lough et al., 2012), since a 5°C increase in acclimation temperature increased the thermal optimum for survival by only $\sim 2^{\circ}\text{C}$ on aggregate. Such an increase in optimum, if it occurred in nature, might buffer those stages from modest warming, but not from extreme events

like heatwaves, which recently warmed regional waters by up to 3°C above average for several months (Oliver et al., 2017). Questions also surround how well acclimation responses to constant temperatures, like we assess here, translate to nature. Natural *Galeolaria* populations may experience relatively stable temperatures on the temporal scale of development (Guillaume et al., 2016), making such responses an appropriate first step for our work. However, assessing responses to fluctuating temperatures, in addition to more extreme temperatures, would deliver more realistic insights into the limits beyond which acclimation no longer prevents death by heat (Ørsted et al., 2022). Another key step would be to assess trade-offs between parents' investments in their own defences against warming versus those of offspring (Waite & Sorte, 2022). Nevertheless, our results imply that warming may unexpectedly benefit ectotherms not yet living at their thermal limits if acclimation induces thermodynamic effects that enhance survival. Our study therefore demonstrates the importance of understanding how acclimation responses aggregate across complex life cycles when predicting the impacts of warming.

AUTHOR CONTRIBUTIONS

Adriana P. Rebolledo, Keyne Monro and Carla M. Sgrò conceived the ideas and designed methodology; Adriana P. Rebolledo collected the data; Adriana P. Rebolledo and Keyne Monro analysed the data, created the graphics and drafted the manuscript; all authors contributed to revisions and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicting interests.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.br15dvf8> (Rebolledo et al., 2023).

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