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Latitudinal variation in the response of tidepool copepods to mean and daily range in temperature

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Abstract. Understanding the evolutionary potential of organisms to adapt to a changing climate, and the fitness consequences of temperature fluctuations, are critical to forecasting the future of biodiversity. Geographic variation among populations in life history response to temperature mean and variability offers one view of the potential for local adaptation to broaden the thermal niche. We used laboratory growth experiments to examine the effects of temperatures between 13°C and 30°C on five life history traits and the intrinsic rate of increase for 15 *Tigriopus californicus* populations distributed over 17° of latitude. Different life history stages showed distinct latitudinal shifts in thermal response, while the temperature of peak population growth consistently declined with increasing latitude. In addition, high-latitude populations grew faster at optimal temperatures but showed steeper fitness declines at high temperature. To test geographic population variation in response to the amplitude of daily thermal fluctuations, we grew three northern and three southern populations and manipulated nightly low and daily high temperatures. We found the lowest fitness overall in the treatment with the highest mean temperature, and the treatment with the greatest variability showed high fitness despite an 8°C greater daily range. Population responses to daily thermal variability were unrelated to latitude of origin. Our results indicate that trade-offs between adaptation to high vs. low temperature, and between growth and maturation vs. survival and fecundity, govern local adaptation along the latitudinal gradient. They also indicate that *T. californicus* populations can maintain fitness over a wide range of daily variability but are more sensitive to small changes in the mean temperature.

Key words: counter-gradient variation; latitudinal compensation; latitudinal gradient; life history; local adaptation; reaction norm; seasonality; temperature mean; temperature variability; thermal niche breadth; *Tigriopus californicus*; trade-offs.

INTRODUCTION

Temperature has pervasive effects on biological processes at all organizational levels (Kordas et al. 2011). For poikilotherms, whose body temperature conforms to that of their environment, temperature determines fundamental biochemical and physiological rates, which in turn affect major life history traits such as survival, growth, and reproduction (Deutsch et al. 2008, Kordas et al. 2011). Since many different traits that can affect fitness are sensitive to temperature, it is not surprising that ectotherms display a variety of adaptive strategies in response to thermal variation (Angilletta et al. 2002). Climate models project that global mean surface temperature for the end of the 21st century will exceed 2°C greater than historic means, and that the magnitude and frequency of thermal extremes will increase (IPCC 2013). Anthropogenic climate change will likely have large impacts on the abundance and distribution of ectotherms. Understanding whether

adaptation can keep pace with a rapidly warming world is key to predicting the consequences of climate change for populations and biodiversity (Carlson et al. 2014).

One approach to estimating thermal sensitivity is to measure thermal performance curves (TPCs) (Huey and Kingsolver 1989). TPCs measure the response of performance traits (e.g., metabolic rate, locomotion, growth, reproduction, or fitness) of individuals reared under a range of constant temperatures. TPCs are typically characterized by a performance increase from a critical minimum temperature (T_{\min}), which then gradually plateaus to a peak optimum temperature (T_{opt}), and finally drops sharply beyond T_{opt} towards a critical thermal maximum (T_{\max}) (Huey and Stevenson 1979). Thermal performance curves have been used to predict the direct effect of temperature on fitness as well as the likely impacts of climate change on a diverse array of ectotherms (Huey et al. 2009, Sinervo et al. 2010, Thomas et al. 2012). Models predict that tropical ectotherms are already living near their thermal optimum, and therefore are at greater risk of extinction from global warming (Deutsch et al. 2008). Ectotherms living below their thermal optimum at higher latitudes are expected to benefit from warmer conditions. However,

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variability on a variety of time scales may expose organisms to periods either below or above their thermal optimum, with potentially major consequences for fitness (Schulte et al. 2011, Kingsolver et al. 2013, Estay et al. 2014, Vasseur et al. 2014).

Our capacity to accurately predict population responses to future climate change is limited when species vary in their response to temperature due to phenotypic plasticity or genetic adaptation (Kelly et al. 2012, Sternberg and Thomas 2014). Local adaptation occurs when spatial variation imposes divergent selection on genetic variation underlying phenotypic traits (Schoville et al. 2012). Populations that are adapted to local conditions will have genotypes with greater fitness in their own habitat than will genotypes from other parts of the species' range (Kawecki and Ebert 2004). As a result, the shape of the thermal performance curve may be altered so that different populations maintain similar fitness across environments that are heterogeneous in space and time. This "latitudinal compensation" is common in many species along latitudinal clines (Yamahira and Conover 2002). Yamahira and Conover (2002: Fig. 1) describe three possible theoretical models for adaptive geographic variation in thermal response. In the first, TPCs are shifted horizontally without changing their breadth or height in response to local mean temperatures (i.e., temperature adaptation). This model suggests a trade-off whereby high-latitude populations perform better at lower temperatures, but are less fit under higher temperatures than low-latitude populations. In the second model, the fitness at T_{opt} increases in high-latitude populations, while the positions of T_{min} , T_{opt} , and T_{max} remain static (i.e., countergradient variation). This type of curve represents an adaptive strategy where greater seasonality favors faster growth during short periods of optimal conditions. The third model combines elements from both of the first two where the height of the peak, T_{min} , T_{opt} , and T_{max} all shift with latitude. Few studies have shown data that allow us to discriminate among the alternative candidate models (Baumann and Conover 2011).

In addition to latitudinal clines in mean temperatures, the seasonal and daily range also shows geographic variation (Janzen 1967). The seasonal range increases with latitude, while the daily range is greatest at low latitude during the winter and at high latitude during the summer (Fig. 1B). This indicates that variable selection may favor local adaptation in thermal niche breadth in addition to tolerance of high or low temperatures. Vasseur et al. (2014) used TPCs for a variety of ectotherms to show that taxa from the temperate zone are more at risk of extinction due to greater thermal variability under climate change than tropical species. However, the potential for evolutionary rescue of species facing climate change through adaptive responses to thermal variability is unknown for most taxa (Buckley and Kingsolver 2012, Carlson et al. 2014).

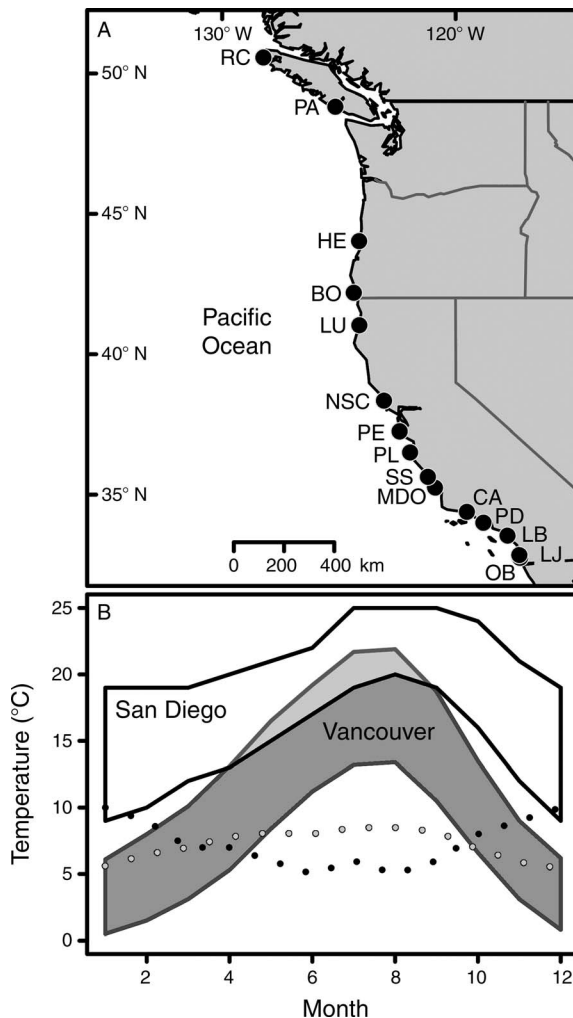


FIG. 1. Sampling locations of *T. californicus* populations (A): Raft Cove, British Columbia (RC) 50°58' N, 128°23' W; Pachena, British Columbia (PA) 48°83' N, 125°15' W; Heceta, Oregon (HE) 44°03' N, 124°13' W; Boardman, Oregon (BO) 42°02' N, 124°36' W; Luffenholtz, California (LU) 41°04' N, 124°12' W; North Salmon Creek, California (NSC) 38°35' N, 123°07' W; Pescadero, California (PE) 37°26' N, 122°04' W; Point Lobos, California (PL) 36°51' N, 121°95' W; San Simeon, California (SS) 35°64' N, 121°19' W; Montaña de Oro, California (MDO) 35°25' N, 120°89' W; Laguna Beach, California (LB) 33°54' N, 117°78' W; La Jolla Cove, California (LJ) 32°85' N, 117°27' W; Ocean Beach, California (OB) 32°75' N, 117°25' W. (B) Recorded monthly mean daily high and low air temperatures at the Vancouver (gray circles) and San Diego (black circles) airports, obtained from their web sites. January is month 1. The upper limits of the bands indicate the average daily high temperature, the lower limits are the nightly lows, and the difference between them is the daily range, which is also shown by the dotted lines.

The harpacticoid copepod *Tigriopus californicus* has become a model system to study local adaptation to thermal variation throughout its geographic range. Populations are distributed across a span of ~35° of latitude, from Baja California, Mexico to southeast Alaska, USA (see Plate 1). *T. californicus* are restricted

to splashpools in the high intertidal and supralittoral zone where tidal immersion is rare. Burton and Lee (1994) showed that gene flow between neighboring populations is low and unlikely to impede local adaptation. A number of studies have documented geographic variation in lethal maximum temperatures (Willett 2010, Kelly et al. 2012, Schoville et al. 2012, Kingsolver et al. 2013, Pereira et al. 2014). However, little is known about whether the other aspects of the thermal response curve (T_{opt} , T_{min} , the slope, T_{max}) also vary with latitude. Willett (2010) found that high-latitude populations had lower T_{max} , but grew faster at temperatures near T_{opt} than more southern populations. This pattern suggests latitudinal variation in peak fitness as well as in T_{max} . However, the effects of thermal environment on the different life history stages and rates that determine population fitness, and their patterns of geographic variation, are unknown.

This study had two aims. First, we tested for variability among *T. californicus* populations in life history parameters grown across a range of temperatures from 13°C to 30°C. We collected 15 populations from Vancouver Island, Canada to San Diego, California and reared individuals in the laboratory under common constant temperatures. Five fitness-related life history traits were measured and the intrinsic rate of population increase was estimated using survivorship and fecundity schedules. The laboratory study sought to test three main predictions: (1) High-latitude populations will have upper thermal limits to fitness at lower temperatures, but higher fitness at low temperatures relative to southern populations, indicating a potential trade-off in adaptation to warm vs. cool climates along a latitudinal gradient. (2) The breadth of the thermal tolerance curve will increase at higher latitudes where populations experience a greater annual temperature range. (3) Fitness at optimal temperatures will increase at high latitudes where shorter growing season selects for more rapid population growth as predicted by the “latitudinal compensation hypothesis” (Yamahira and Conover 2002). Our experiment covered the complete life cycle of *T. californicus*, allowing us to determine how populations have diverged in the response of different life history traits to temperature along a broad latitudinal gradient.

Our second aim was to examine population differences in sensitivities to elevated daily temperature mean and variation. High-latitude populations experience a more pronounced seasonal cycle in temperature, and the amplitude of the daily fluctuation also shifts seasonally (Fig. 1). We grew six populations (three northern and three southern) outdoors in bottles submerged in tanks with different thermal masses (as determined by water depth) with and without shading to manipulate the daily high and low temperatures. We tested the following predictions: (1) Population growth will be affected differently by variation in the daily high, low, and mean temperatures because of the nonlinearity of the thermal response curve (Vasseur et al. 2014). And (2) northern

populations will be less affected by an increased daily thermal range than southern populations as they experience greater temperature changes throughout the day during the summer (when our experiment was performed) in their native environment (Fig. 1). The results of these two experiments provide insights into how the life histories of geographically dispersed *T. californicus* populations vary in response to high and low temperatures, and to variation in the daily temperature range.

METHODS

Field collection and stock cultures

We collected and established laboratory cultures of 15 *T. californicus* populations across a broad latitudinal range of >17° from Southern California to Canada in June of 2011 (Fig. 1A). In the laboratory, copepods were maintained in 250-mL Nalgene bottles filled with 100 mL of filtered (Whatman GF/F; porosity, 0.22 µm; Whatman Incorporated, Florham Park, New Jersey, USA) seawater from Scripps Institute of Oceanography, La Jolla, California and maintained at 20°C under a 12-hour photoperiod. Copepods were fed powdered *Spirulina* (Spectrum S1493) in solution at 10 mg/mL filtered seawater weekly, and filtered seawater was changed occasionally. Cultures were maintained under similar conditions for 1–2 years prior to the start of our experiments, which should be sufficient to eliminate maternal effects that confound local adaptation (Kawecki and Ebert 2004).

Laboratory experiment: juvenile survival and somatic growth

To initiate an experimental population, we first randomly sampled 24 early gravid-stage females (females carrying a green egg sac) from our stock culture for each of our 15 populations, and then isolated each female into 9-mL 6-well plates. Wells were filled with 3 mL of filtered seawater and maintained at 20°C under a 12-hour photoperiod with excess food (40 mg *Spirulina* in solution) to discourage cannibalism. After allowing two days to hatch, four nauplii from each female were randomly assigned to one of four temperature treatments (15°, 20°, 25°, and 30°C) and transferred individually to 3-mL 24-well plates containing 1.5 mL of juvenile medium (0.02 g *Spirulina*/L of filtered seawater). Plates were placed into incubators and individuals were transferred into new well plates with fresh medium after 24 hours, and then at every other day thereafter for two weeks. During transfer, any immobile juveniles were identified to be dead if the appendages and gut remain motionless during 10 seconds of light brushing of the antenna with a dissecting pin. We measured juvenile survival as the number of days survived.

The presence of molted exuviae was checked in old well plates between transfers. Exuviae were photographed using a Leica (Leica Microsystems, Wetzlar, Germany) DFC 296 camera mounted on a Leica M125



PLATE 1. Examples of high intertidal rock pool habitats in Oregon (USA) where copepods were collected for these experiments. Photo credits: J. B. Shurin.

stereomicroscope. Photos were processed through Leica Application Suite V3.5.0 and the anteroposterior exuvial length, excluding the antenna and caudal ramus, was measured using ImageJ version 1.46r (Abramoff et al. 2004, Schneider et al. 2012). Since multiple exuviae may be left by juveniles that molt more than once, the smallest exuvia observed after 24 hours was measured as the initial size. Only the largest exuvia was measured for subsequent samples. Juvenile somatic growth rate was approximated using the following equation:

$$\frac{\sum L_x - L_1}{\sum x - 1} \quad (1)$$

where L_1 is the initial length (smallest exuvia after 24 h) and L_x is the largest exuvial length at day x .

Laboratory experiment: adult survival, time to maturity, and fecundity

Our procedure for initiating experimental nauplii for the adult common garden experiment was similar to that used for juveniles, except that two populations (NSC and LB; Fig. 1A) were excluded due to low stock culture density. For each of our 13 populations, four newly hatched nauplii from each of 20 mothers were randomly split between four 250-mL Nalgene bottles containing 100 mL of filtered seawater and 5 mg/week of *Spirulina* in solution. The four bottles for each population were placed separately into 13°, 20°, 23°, or 25°C incubators. We used a lower range of temperatures compared to the juvenile common garden experiment to ensure that the 20 nauplii in each of the 25°C bottles survived long enough to mate and produce gravid adults. Bottles were checked daily to measure time to maturity as the number of days for individuals to reach early gravid stage. This

continued until 5 gravid females were achieved for each population and temperature.

Gravid females were pipetted immediately from the bottles into 9-mL 6-well plates containing 3 mL of adult growth medium (0.1 g *Spirulina*/L of filtered seawater) and returned to their corresponding temperature treatment. A total of five replicates was used for each population and treatment. Egg sac development was checked while adults were transferred daily to new well plates with fresh medium. Newly hatched nauplii were counted by pipetting, and lifetime fecundity was measured as the total offspring produced for each female. Survival was recorded similar to the procedure used for juvenile survival. The experiment ran until the death of the last surviving adult at 131 days.

Laboratory experiment: intrinsic rate of population increase

The intrinsic rate of population increase (r) was approximated using two key components of fitness, net reproductive rate (R_0) and generation time (G), as follows:

$$R_0 = \sum_x^{\infty} x l_x m_x \quad (2)$$

$$G = \frac{\sum_{x=0}^{\infty} x l_x m_x}{\sum_{x=0}^{\infty} l_x m_x} \quad (3)$$

$$r \approx \frac{\ln(R_0)}{G} \quad (4)$$

where l_x is the survivorship or proportion of females surviving from birth to day x , m_x is age-specific fecundity or average number of offspring produced at day x , and ω is female longevity. To obtain the exact values of r , approximated values of r from Eq. 4 were corrected by the iterative bisection method from Euler-Lotka's equation (see Jha et al. 2012) with age indexed from zero (i.e., $l_0 = 1$)

$$\sum_{x=0}^{\omega} l_x m_x e^{-rx} = 1. \quad (5)$$

Mesocosm experiment

The mesocosm experiment examined the population growth response of copepods from northern and southern latitudes to variation in the mean and amplitude of daily temperature variation. It was performed between 29 June and 17 August 2013. We used a 2×2 factorial design to manipulate the daily high and the nightly low temperature using a combination of shade cloth and water depth variation. At the UC–San Diego Biological Field Station, we established four treatments using 400-L plastic stock tanks. Two tanks were completely filled with well water and the other two were filled to ~ 80 L. One tank of each depth was covered with two layers of shade cloth to limit irradiance. Temperature in the tanks was recorded with Hobo Data Loggers (Onset Computer Corporation, Bourne, Massachusetts, USA). The shading treatment mainly affected the daily high, while the depth treatment altered the nightly low temperature (see *Results*). The tanks served as water baths to buffer the daily thermal cycle, with the shallow tanks showing a greater daily range than the deep tanks as a result of smaller thermal mass. However, as the copepods were all enclosed in opaque 250-ml Nalgene bottles submerged within the tanks, the volume of their habitat was constant across treatments.

Three northern (RC, PA, HE) and three southern (PL, SS, OB) populations were chosen from our collection of 15 (Fig. 1A). Since our collection included more southern than northern populations, we divided our latitudinal range in half and selected populations from the south at random. Each experimental population was initiated in the laboratory by inoculating 20 newly hatched nauplii in 200 mL of filtered seawater within the 250-mL bottles. There were three replicates per treatment. Bottles were capped tightly and enclosed in minnow traps to maintain similar heights at the bottom of the tanks in random configurations. The bottles had 50 mL of headspace, which was refreshed during weekly sampling dates, to maintain aeration and prevent anoxia.

The populations in the experiment were collected and brought back to the laboratory once a week for a total of seven weeks to be fed *Spirulina* under ad libitum

conditions and counted based on their life stage (i.e., nauplius, copepodid, adult male, adult female, and gravid female). If <40 individuals were present, an exhaustive count was made by filtering copepods through a 50- μ m mesh before placing them into a petri dish to be examined under a dissecting microscope. Subsampling was required when densities became unmanageably high. Because copepods were keen to avoid being captured, bottles were swirled to homogenize animals before a 10-mL subsample was taken. The same volume subsample was repeated if the cumulative density of five individuals was not achieved in the previous attempts, but no more than 40 mL was pipetted into the petri dish.

Statistical analysis

All statistical analyses were performed using the statistical program R version 3.1.0 (R Development Core Team 2014). Our five life history traits and fitness (r) were fit to a second-order polynomial using the full model: $y = L + T + T^2 + L \times T + L \times T^2$, where y is the predicted parameter, L is latitude, T is the first order of temperature, and T^2 is the second order of temperature. A second-order term was included because biological processes often show a unimodal relationship with temperature (Kingsolver et al. 2013). Model simplification was based on minimizing Akaike's Information Criterion (AIC) using backward stepwise procedure with the stepAIC function in the MASS package (Venables and Ripley 2002) in R. After checking for normality using a Shapiro–Wilk test and for homogeneity with a Fligner–Killeen test, it was necessary to square-root transform our abundance data in our mesocosm experiment. We then used a three-way analysis of variance (ANOVA) to test for population differences in abundance in response to the effects of shading and water depth.

RESULTS

Laboratory experiment

Common environment experiments revealed that all five life history traits and fitness (r) varied significantly with latitude and temperature (Fig. 2, Table 1). In addition, interactions involving latitude and either the first- or second-order terms for temperature were significant for all variables except adult survival and lifetime fecundity, indicating that the shape of the thermal response varied with latitude in most cases. The best fit models are shown as heat maps for temperature and latitude in Fig. 2. Juvenile and adult survival varied inversely with temperature and latitude (Fig. 2A, C). Plots of the raw values for each population are shown in the Appendix (Figs. A1–A5), as is the result of the model-averaging approach to testing the effects of latitude and temperature. Juvenile somatic growth peaked at intermediate temperatures and increased with latitude at all temperatures (Fig. 2B). Time to maturity was shortest between about 20°C to 25°C in southern populations, and between about 17°C to 25°C

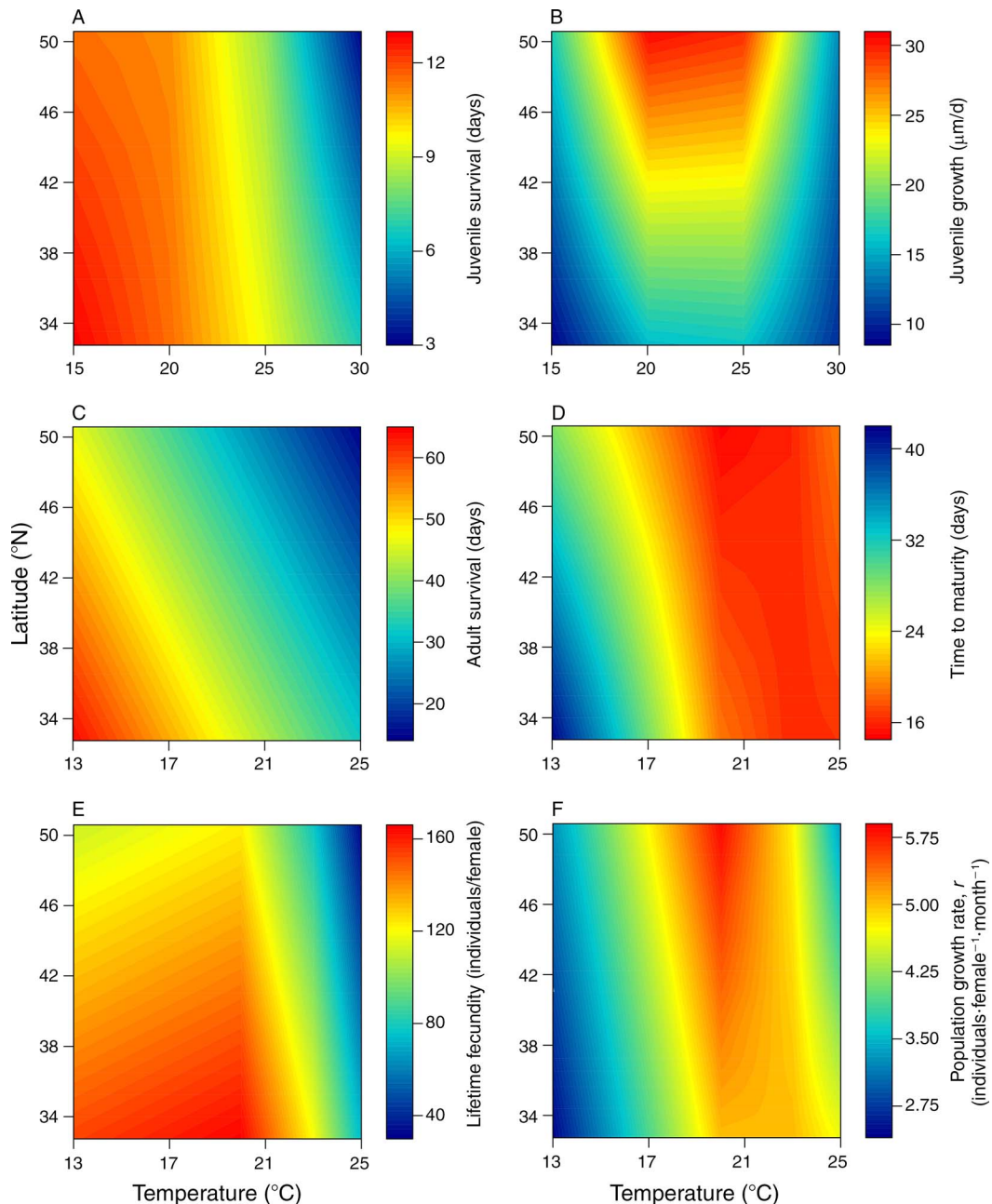


FIG. 2. Heatmaps of (A) juvenile survival (days) and (B) growth ($\mu\text{m}/\text{d}$), (C) adult survival (days), (D) time to maturity (days), (E) lifetime fecundity (individuals/female), and (F) intrinsic rate of population increase (individuals·female⁻¹·month⁻¹). Trait values, shown on the color scale, were predicted as a function of temperature and latitude using the model terms in Table 1.

in northern populations (Fig. 2D). Lifetime fecundity peaked at intermediate temperatures for populations from low latitudes, and the decline at high temperatures shifted to lower temperatures with increasing latitude (Fig. 2E). The overall thermal response of fitness shifted consistently towards a lower range of temperatures with increasing latitude. In addition, growth of high-latitude populations was faster at optimal temperatures but showed steeper declines at high temperature.

Mesocosm experiment

The effect of shading and water depth on mesocosm conditions in terms of their daily mean, range, maximum, and minimum temperatures are shown in Fig. 3. The unshaded tanks had a mean temperature around 1.06°C higher than the shaded tanks while the shallow tanks were $\sim 0.75^\circ\text{C}$ cooler than the deep tanks (Fig. 3A). Additionally, the highest mean temperature was in the unshaded deep tanks at 24.5°C. The daily temper-

TABLE 1. Results of stepwise multiple regression analyses between latitude (L), first-order temperature (T), second-order temperature (T^2), and their interactions for *T. californicus* life history traits.

Trait	Model term	Estimate	SE	F	P
Juvenile survival	Intercept	38.930	11.494	11.471	<0.001
	L	-0.820	0.296	7.686	0.006
	T	-2.356	1.069	4.858	0.028
	T^2	0.049	0.024	4.261	0.039
	$L \times T$	0.078	0.028	8.008	0.005
	$L \times T^2$	-0.002	0.001	9.787	0.002
Juvenile growth	Intercept	61.124	28.891	4.476	0.035
	L	-3.444	0.741	21.613	<0.001
	T	-7.086	2.723	6.771	0.009
	T^2	0.173	0.061	7.970	0.005
	$L \times T$	0.399	0.070	32.643	<0.001
	$L \times T^2$	-0.009	0.002	34.762	<0.001
Adult survival	Intercept	126.540	11.856	113.950	<0.001
	L	-0.918	0.256	12.855	<0.001
	T	-2.552	0.330	59.851	<0.001
	R^2	0.237			
	Time to maturity	Intercept	207.796	17.306	144.168
Time to maturity	L	-1.816	0.361	25.297	<0.001
	T	-13.996	1.356	106.603	<0.001
	T^2	0.244	0.0316	59.766	<0.001
	$L \times T$	0.080	0.0175	20.962	<0.001
	R^2	0.643			
	Lifetime fecundity	Intercept	-199.864	167.052	1.431
Lifetime fecundity	L	-2.209	1.216	3.301	0.071
	T	52.978	18.289	8.392	0.004
	T^2	-1.561	0.491	10.110	0.002
	R^2	0.081			
	Intrinsic rate of increase	Intercept	3.825	2.191	3.048
Intrinsic rate of increase	L	-0.480	0.056	72.884	<0.001
	T	-0.610	0.253	5.827	0.016
	T^2	0.030	0.007	18.9	<0.001
	$L \times T$	0.067	0.007	106.578	<0.001
	$L \times T^2$	-0.002	0.000	134.119	<0.001
	R^2	0.644			

Notes: Model terms retained if removal resulted in \geq AIC using backward stepwise procedure. SE is standard error; R^2 is adjusted coefficient of determination; $N=24$ for juvenile stage and $N=5$ for adult stage.

ature range was highest (11.90°C) in the unshaded shallow tanks, intermediate in the shaded shallow (7.04°C) and deep (7.14°C) tanks, and lowest in the shaded deep tanks (4.66°C) (Fig. 3B).

Population growth varied among populations and was affected by the shading treatment but not the depth treatment (Table 2). After seven weeks, copepods grown in unshaded treatments were significantly less abundant than those grown in shaded treatments (ANOVA, $F_{1,48} = 12.3$, $P < 0.001$) with an overall reduction of $\sim 50\%$ from 465.5 ± 57.4 copepods (mean \pm SD) to 245.4 ± 69.6 copepods (Fig. 4). Populations varied in their response to daily thermal variability (ANOVA, $F_{1,48} = 4.97$, $P < 0.001$), but these differences were unrelated to latitude of origin (Fig. 4, Table 2). In populations B, C, and E, the lowest abundance was observed in the unshaded deep treatment, while in population A, abundance was lowest in both unshaded treatments. In D and F, abundance was similar among all treatments. The unshaded deep treatment had the highest mean temperature (Fig. 3A), while the unshaded

shallow tank had the highest daily maximum and daily range. Deep treatments resulted in an overall increase in the average daily minimum temperature from 19.4°C to 21.2°C (Fig. 3D).

DISCUSSION

We identified two key shifts in the thermal response of *T. californicus* copepods with latitude along the North Pacific coast. First, fitness of high-latitude populations is generally higher at cold temperatures and lower at warm temperatures than southern populations, indicating a potential trade-off between performances in warm vs. cold conditions. High-latitude populations experience a greater annual temperature range, and therefore might be expected to have wider tolerance. However, we saw no indication of a broadening of the thermal niche at high latitude as both the increasing and declining phases of the thermal response curve shifted lower. Instead, we found that fitness at the temperature optimum increased at high latitude, consistent with the idea that short growing seasons favor faster population growth (Ya-

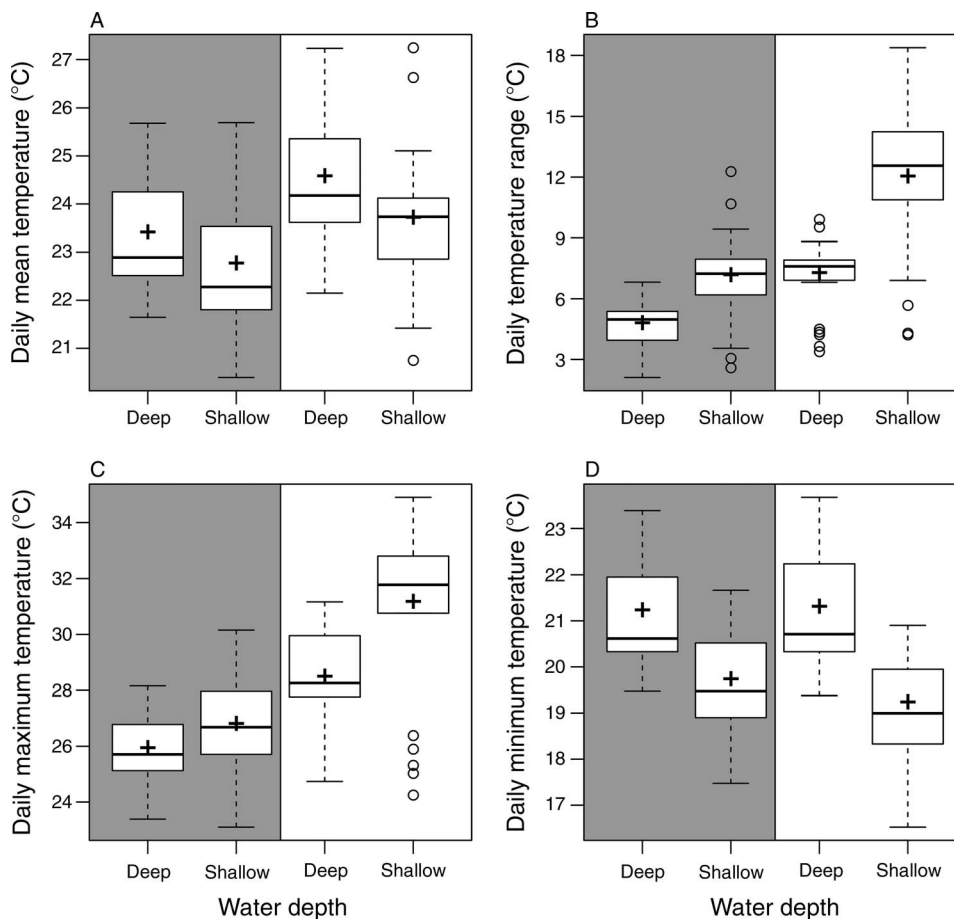


FIG. 3. Boxplots showing the median, quartiles, and whiskers showing 1.5 times interquartile range of daily temperature mean (A), range (B), maximum (C), and minimum (D) under experimental mesocosms with different water depth and shading combinations. Boxplots in gray and white regions are shaded and unshaded treatments, respectively. Plus symbols indicate means and circles are outliers.

mahira and Conover 2002). Second, our data are also consistent with a life history trade-off between fast growth and maturation vs. high survival and lifetime fecundity. Northern populations show accelerated life cycles relative to those from the south, but experience lower survival. In addition, the mesocosm experiment found that *T. californicus* populations showed the lowest fitness at high daily mean temperatures, but maintained relatively high fitness in the treatment with the largest daily range. This result contradicted our expectation that large daily fluctuations in temperature should reduce population growth, and suggests that physiological mechanisms maintain fitness despite daily short-term exposure to stressful temperatures. The population response to mean temperatures shifts with latitude, but the breadth of thermal tolerance, both in terms of the mean and daily range, was surprisingly consistent.

The thermal response curves of different life history stages showed distinct latitudinal patterns. Northern populations showed faster somatic growth and maturity, but lower survival and fecundity. Edmands and Harri-

son (2003) also found that northern *T. californicus* populations (Vancouver Island and Washington) developed faster and became larger than those from southern California. Our results also indicate genetic differences where northern populations grew and developed faster at optimal temperatures. The physiological mechanism linking growth and development rates to survival

TABLE 2. ANOVA table of *T. californicus* abundance as a function of population (Pop), depth, and shading.

Effect	df	SS	MS	F	P
Pop	5	1268.9	253.8	4.966	<0.001
Depth	1	130.1	130.1	2.546	0.117
Shading	1	628.9	628.9	12.307	<0.001
Pop × depth	5	236.0	47.2	0.924	0.474
Pop × shading	5	189.7	37.9	0.742	0.596
Depth × shading	1	71.8	71.8	1.404	0.242
Pop × depth × shading	5	97.5	19.5	0.382	0.859
Residual	48	2453.0	51.1		

Notes: df are degrees of freedom; SS are sums of squares; MS are mean squares.

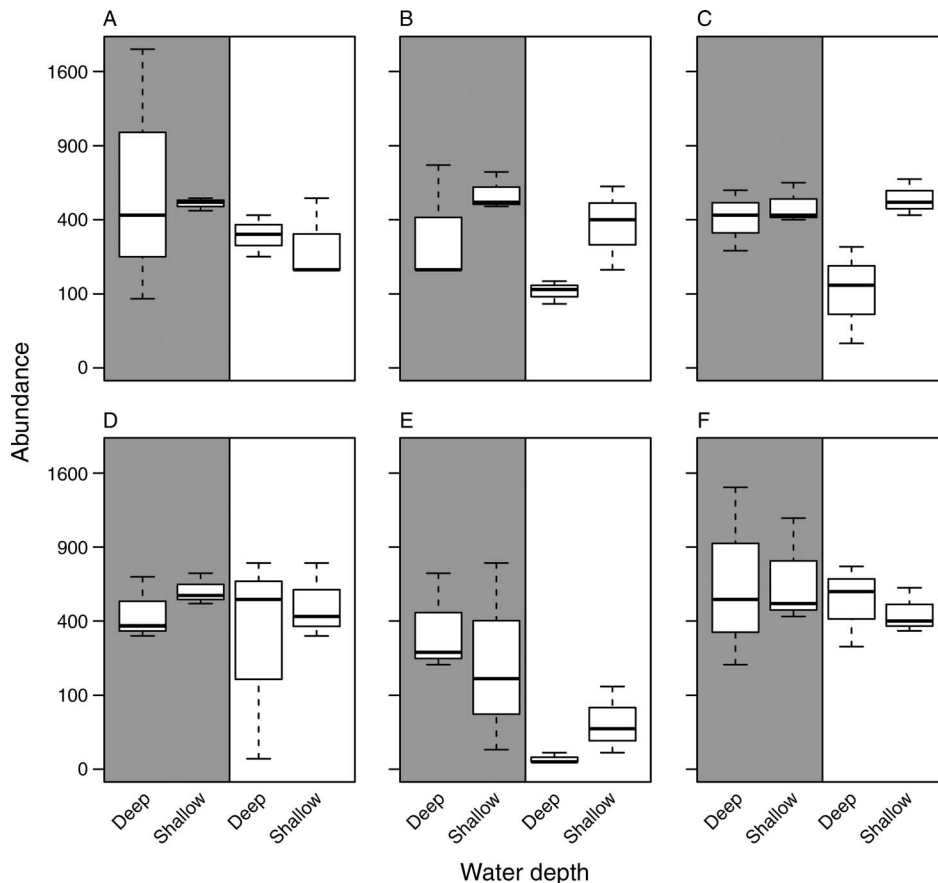


FIG. 4. Boxplots showing the median, minimum, maximum, and quartiles of abundance for northern (A–C) and southern (D–F) *T. californicus* populations after seven weeks in experimental mesocosms with different water depth and shading combinations. The populations used are as follows: (A) RC, (B) PA, (C) HE, (D) PL, (E) SS, and (F) OB. Boxplots in gray and white regions are shaded and unshaded treatments, respectively. Note the nonlinear scale on the y-axes.

remains unknown; however, our results and those of Edmands and Harrison (2003) and Willett (2010) are consistent in suggesting that northern climates may select for fast life history strategies with rapid growth and maturity at a cost of reduced survival and fecundity.

The latitudinal patterns we observed in growth may be an example of counter-gradient variation (CnGV) (see Gardiner et al. 2010: Fig. 1), where a physiological trait evolves in opposition to the expected ecological response along an environmental gradient. For example, northern populations may show metabolic compensation to maintain higher growth under colder conditions. Rapid population growth is expected to be favored at higher latitudes where long periods of low temperatures delay completion of earlier vulnerable juvenile life stages (Lindgren and Laurila 2009, McAllen and Brennan 2009) or growth to a minimum size required for reaching reproductive maturity (Arendt 1997). Our results from juveniles reared under common-environment conditions provide evidence that growth potential varies inversely with length of the growing season along latitudinal gradients. Examples of CnGV have been shown for

many ectotherms (Lindgren and Laurila 2009), including the estuarine harpacticoid copepod *Scottolana canadensis* (Lonsdale and Levinton 1985), terrestrial snails (Gaitán-Espitia and Nespolo 2014), and fish (Baumann and Conover 2011). However, to our knowledge, no studies have demonstrated CnGV in *T. californicus*. Further research is necessary to determine the physiological mechanisms behind CnGV.

We found that northern populations of *T. californicus* show a pattern of fast growth and early maturity and reduced survival and fecundity. Willett (2010) also found that survival under acute and chronic high-temperature stress increased at low latitude. Our results show that, in addition to thermal adaptation at T_{max} , the pattern of survival response at moderate and low temperatures also varied inversely with latitude. Willett (2010) also measured competition between two northern and southern population pairs from California and showed that northern copepods had a relative fitness advantage at 16°C. At the highest temperature tested (24°C average), southern copepods gained the fitness edge over their competitors. The mechanism underlying

this potential trade-off is unknown (Lindgren and Laurila 2009), but similar to the pattern shown by Yamahira and Conover (2002) for fishes. They propose that fast growth and early reproduction should be favored in northern populations due to reduced growing season length. Copepods, which mature in a matter of 2–4 weeks at most temperatures and are multivoltine (Dybdahl 1994, Kelly et al. 2012), may be less sensitive to the length of time it takes to complete their life cycle. However, our results indicate a general tendency toward a faster pace of living and reduced investment in survival and lifetime fecundity with increasing latitude.

A variety of conceptual models have been proposed to explain patterns of temperature response in marine zooplankton (for review see Dam 2013). A specialist–generalist model predicts a widening of the thermal niche breadth for northern and mid-latitude organisms that experience greater seasonality (Clarke and Gaston 2006). Organisms that inhabit more stable temperature environments are expected to have a narrower thermal niche but higher fitness around their optimum (Gilchrist 1995). The thermal fitness breadth of *T. californicus* in our laboratory experiment, however, was similar among populations. Instead, the fitness pattern we observed is consistent with the third model proposed by Yamahira and Conover (2002), where all phases of the temperature response curve shift downward and the peak fitness becomes greater at high latitude. We saw no sign of a broadening of the thermal response curve (a greater difference between T_{\min} and T_{\max}), even though high-latitude populations experience a greater seasonal range.

We also found that lifetime fecundity declined with temperature, and at high latitude, likely as a result of reduced survival. While the effect of temperature on fecundity was nonlinear, declining at both extremes, there was no significant interaction with latitude of origin of the population, suggesting that the shape of the fecundity–temperature curve was constant across latitude. Egloff (1966) observed a similar thermal response pattern where egg mortality increased below 10°C and above 25°C. Although lifetime fecundity increased at low latitude, the latitudinal term used in the model was only marginally significant (Table 1). A lifetime fecundity of about 120–160 nauplii can be expected under optimal thermal conditions for *T. californicus* fed ad libitum. Vittor (1971) showed a maximum of 300 progeny over a lifetime, while we observed one female that produced 579 offspring. Our measure of lifetime fecundity should be accurate for *T. californicus* females, which, unlike males, mate only once (Burton 1985). However, females in natural pools, particularly those that contain dense populations, likely produce fewer offspring than in the laboratory due to density-dependent factors. For example, pools can reach population densities of ~20 000 copepods/L (Powlik 1998); therefore, realized fecundity in nature is likely to be much lower than in our experiments.

Our field experiment showed that *T. californicus* populations can maintain fitness even when the amplitude of the daily fitness cycle is large enough to encounter periods where we would expect reduced fitness due to both high and low temperatures. The shading treatment, but not water depth, had a significant effect on fitness in the field experiment. The unshaded, shallow tank had a daily range of ~5°C greater than either the unshaded deep or the shaded shallow treatments, and around 8°C greater than the shaded deep tank. It also experienced daily highs above 34°C and nightly lows as low as 17°C. In the laboratory, we observed reductions in fitness at constant temperatures above ~23°C and below 19°C for southern populations. Acute lethal temperatures for *T. californicus* are typically around 38°C (Kontogiannis 1975, Willett 2010). We would therefore expect to see low fitness in the shallow, unshaded treatment; however, this was not the case. This result indicates that the time frame of thermal variability is important to the fitness consequences, as copepods thrived despite regular exposure to a few hours of temperatures near their lethal thermal limit. Physiological mechanisms for coping with brief periods of thermal stress may therefore maintain fitness with high-frequency daily cycles that include temperatures near the upper limits.

We observed the lowest population growth in the deep, unshaded treatment, which had the highest daily mean temperature but a relatively narrow daily range. The difference in daily mean among treatments was remarkably small. The daily average temperature in the shaded treatment was only ~1°C cooler than the unshaded, and the deep unshaded treatment was <1°C warmer on average than the shallow. However, the daily high was 1°–5°C higher in the unshaded than the shaded treatment (Fig. 3C). The treatment with the lowest overall fitness was not the one with the highest average daily high (shallow, unshaded), but the highest daily mean (deep, unshaded). This result also indicates that the timeframe of exposure to high temperatures is important to determining their fitness consequences. Chronic exposure to higher temperatures reduced population growth to a greater extent than regular shorter-term exposure to temperatures near the lethal limit. In nature, variation in daily thermal regime likely occurs as a function of latitude as well as local features such as pool volume, surface area, and aspect. Further experiments are needed to determine how thermal response curves measured in the laboratory under constant conditions reflect fitness effects of temperature fluctuations on daily, seasonal, and longer time scales.

Our study supports a growing body of evidence that the thermal responses of physiological and life history rates show geographic variation within species that reflects the temperature regimes of different environments. For instance, Higgins et al. (2014) showed that larvae of two butterfly species from high-elevation populations fed at higher rates and had higher

maximum feeding temperatures than those from lower elevations. Sanford and Kelly (2011) and Sorte et al. (2011) reviewed studies of local adaptation in marine invertebrates and show a number of examples of geographic variation in response to temperature consistent with local adaptation. Most of these studies examine effects in terms of growth, survival, or reproduction, but do not put these together into a stage-structured model to predict effects on population growth. In addition, most studies maintain constant temperatures in laboratory conditions and have not tested the effects of the amplitude of temperature fluctuations that occur as a result of microhabitat variability, for instance due to differences in the size of tide pools. Our mesocosm experiment shows that the time scale of temperature variation has important implications for fitness consequences. Further experiments testing the effects of temperature variation on different time scales are needed to understand how evolution shapes organismal responses to changing thermal regimes.

In summary, our results indicate two main life history trade-offs that govern the fitness response of *T. californicus* populations to temperature along a latitudinal gradient. First, high-latitude populations perform better at low temperatures and worse under warm conditions. The entire fitness response curve shifts to lower temperatures with increasing latitude, with no indication of a broadening of the thermal niche. Second, high-latitude populations generally show fast growth and maturity but reduced survival and fecundity compared to low-latitude populations growing at the same temperatures. High-latitude populations also show higher peak fitness around the thermal optimum, consistent with counter-gradient genetic variation (Gardiner et al. 2010). Finally, the mesocosm experiment showed increased population growth when the daily average temperature was reduced by only 1°C by shading. However, populations maintained high fitness in the treatment with the greatest thermal amplitude and the highest daily maximum, indicating little effect of short exposure to temperatures that greatly reduce fitness under chronic exposure. Instead, small changes in the daily mean temperature may be more important. Our results indicate that a suite of life history traits show shifts in their temperature response with latitude, and that high-latitude populations show no signs of broader thermal niches despite living in more seasonally variable environments.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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