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

A Thesis submitted in partial satisfaction of the requirements for the degree
Master of Science

in

Biology

by

Brian C. Hong

Committee in charge:

Professor Jonathan B. Shurin
Professor Ronald S. Burton
Professor Kaustuv Roy

2014

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The Thesis of Brian C. Hong is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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University of California, San Diego

2014

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ABSTRACT OF THE THESIS

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

by

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Master of Science in Biology

University of California, San Diego, 2014

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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 and 25°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 tradeoffs 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.

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 & 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 (CT_{min}), which then gradually plateaus to a peak optimum temperature (T_{opt}), and finally drops sharply beyond T_{opt} towards a critical thermal maximum (CT_{max}) (Huey & 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, 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, Estay et al. 2013, Kingsolver et al. 2013, 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 & Thomas 2014). Local adaptation occurs when spatial variation in natural selection produces geographic 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 in other parts of their range (Kawecki & 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 & Conover 2002). Yamahira & Conover (2002) 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 latitudes 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 local adaptation in population response to thermal variability is unknown for most taxa (Buckley & Kingsolver 2012, Carlson et al. 2014).

The harpacticoid copepod *Tigriopus californicus* has become a model system to study local adaptation to thermal variation throughout its geographic range. Populations are distributed broadly across a span of $\sim 35^\circ$ of latitude, from Baja California, Mexico to southeast Alaska, USA. *T. californicus* are restricted to splashpools in the high intertidal and supralittoral zone where tidal immersion is rare. Burton & 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, Sarà et al. 2011, Kelly et al. 2012, Schoville et al. 2012, Kingsolver et al. 2013, Pereira et al. 2013). 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 across a range of temperatures from 13-25°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 lab study sought to document geographic variation in the temperature response of life history components of fitness, and to identify potential tradeoffs among alternative life history strategies along a latitudinal cline. 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. 1B). We grew six populations 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. The results of these two experiments provide insights into how the life histories of *T. californicus* populations vary in response to high and low temperatures, and to variation in the daily temperature range.

Materials and Methods

Field Collection and Stock Cultures

We collected and established laboratory cultures of fifteen *T. californicus* populations across a broad latitudinal range of over 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) seawater from Scripps Institute of Oceanography, La Jolla, CA and maintained at 20°C under a 12-hour photoperiod. Copepods were fed powdered *Spirulina* (Spectrum S1493) in solution at 10 mg per mL filtered seawater weekly and filtered seawater was changed occasionally. Cultures were maintained under similar conditions for 1 to 2 years prior to the start of our common garden and mesocosm experiment, which should be more than sufficient to eliminate maternal effects that confound local adaptation (Kawecki & 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⁻¹ 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 immobilized 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 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). 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:

$$\frac{\sum L_x - L_1}{\sum x - 1} \quad \text{eqn 1}$$

where L_1 is the initial length (smallest exuvia after 24 hrs) 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⁻¹ 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⁻¹ filtered seawater) and returned to their corresponding temperature treatment. A total of 5 replicates were 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:

$$R_0 = \sum_{x=0}^{\omega} x l_x m_x \quad \text{eqn 2}$$

$$G = \frac{\sum_{x=0}^{\omega} x l_x m_x}{\sum_{x=0}^{\omega} l_x m_x} \quad \text{eqn 3}$$

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

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 equation 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., $l_0 = 1$):

$$\sum_{x=0}^{\omega} l_x m_x e^{-rx} = 1 \quad \text{eqn 5}$$

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. We used a 2x2 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 100 gallon plastic stock tanks. Two tanks were completely filled with well water and the other two were filled to approximately 20 gal. 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, Bourne, Massachusetts, USA). The shading treatment mainly affected the daily high while the depth treatment altered the nightly low temperature. Figure 3 shows the mean (A), daily range (B), maximum (C), and minimum (D) temperatures in the four treatments. The unshaded tanks had a mean temperature around 1.06°C higher than the shaded tanks, and the shallow tanks were ~0.75°C cooler than the deep tanks (Fig. 3a). The daily temperature 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).

Three northern (RC, PA, HE) and three southern (PL, SS, OB) populations were chosen from our collection of fifteen (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 250 mL Nalgene bottles with 20 newly hatched nauplii in 200 mL of filtered seawater. 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 7 weeks to be fed *Spirulina* under ad libitum conditions and counted based on their life stage (i.e., nauplii, copepodid, adult male, adult female, and gravid female). If less than 40 individuals were present, an exhaustive count was made by filtering copepods through a 50 μm mesh before placing them into a petri dish to be examined under a dissecting scope. 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 5 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. Model simplification was based on minimizing Akaike's Information Criterion (AIC) using backward stepwise procedure with the stepAIC function in the MASS package (Venables & 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). Juvenile somatic growth peaked at intermediate temperatures and increased with latitude at all temperatures (Fig. 2B). Time to maturity was shortest between about 20-25°C in southern populations, and between around 17-25°C in northern populations (Fig. 2D). Lifetime fecundity peaked at intermediate temperatures and at low latitudes, and the decline at high temperatures shifted to the left 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 Figure 3. The unshaded tanks had a mean temperature around 1.06°C higher than the shaded tanks while the shallow tanks were ~0.75°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 temperature 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 7 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 ~50% from 465.5 ± 57.4 SD to 245.4 ± 69.6 SD (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 found distinct latitudinal shifts in five major fitness related life history traits among 15 *T. californicus* populations reared under a range of common temperatures. Juvenile and adult survival, and time to maturity varied inversely with temperature and latitude, while juvenile somatic growth and adult fecundity peaked at intermediate temperatures. Common environment experiments also revealed that the temperature of peak population growth consistently declined with increasing latitude. Additionally, growth of high latitude populations was faster at optimal temperatures but showed steeper declines at high temperature. These results suggest that life history tradeoffs underlie local adaptation to high and low temperatures such that fitness at high temperatures declines at high latitude while fitness at low temperatures increases. In addition, *T. californicus* populations grown under different thermal regimes showed greatest sensitivity to high mean temperatures, but maintained relatively high abundance under high thermal variability. Populations varied in their response to daily thermal variability, but these differences were unrelated to latitude of origin. Our results show local genetic variation along a latitudinal gradient in the life history and fitness response to both the mean and daily range of temperature.

Our results indicate that life history tradeoffs underlie the latitudinal shift in thermal response of fitness. Northern populations showed faster somatic growth and maturity, but lower survival and fecundity. Edmands & Harrison (2003) also found that *T. californicus* individuals from northern populations (between Vancouver and Washington) developed faster and became larger than those from southern California in the field. Environmental conditions including food availability, dissolved oxygen, and temperature may have contributed to the patterns they observed, and our results indicate that genetic differences also likely played a role. Our results indicate that geographic genetic variation is also responsible for the latitudinal cline in phenotypic traits. Northern climates 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 Fig. 1C of Gardiner et al. 2010), 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 capacities under colder conditions. Having the capability to grow rapidly would be advantageous at higher latitudes where long periods of low temperatures would otherwise delay completion of earlier vulnerable juvenile life stages (Lindgren & Laurila 2009, McAllen & Brennan 2009) or growth to a required minimum size before reaching reproductive maturity (Arendt 1997). Our results from juveniles reared under common-garden conditions provide evidence that growth potential varies inversely with length of the growing season along latitudinal gradients. Examples of CnGV are common for many ectotherms (Lindgren & Laurila 2009), including the estuarine harpacticoid copepod *Scottolana canadensis* (Lonsdale & Levinton 1985), terrestrial snails (Gaitán-Espitia & Nespolo 2014), and fish (Baumann & Conover 2011). However, to our knowledge, no studies have been conducted to specifically address CnGV in *T. californicus*. Further research is necessary to determine if CnGV is apparent in this copepod species, and the potential physiological mechanisms behind it. For example, greater oxygen consumption would be expected for northern copepods if there is in fact metabolic compensation (Gardiner et al. 2010).

Northern populations of *T. californicus* show a pattern of adaptation that trades off fast growth and early maturity for reduced survival and fecundity. Willett (2010) found that survival under acute and chronic high temperature stress increased with decreasing 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 fitness advantage that allowed them to dominate at a low temperature of 16°C. At the highest temperature tested (24°C average), southern copepods gained the fitness

edge over their competitors. The outcome of the winner was less clear at an intermediate temperature of 20C, but tended to favor the northern population in one pair. The mechanism underlying this tradeoff is unknown (Lindgren & Laurila 2009), but the pattern is similar to that shown by Yamahira & 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 wide variety of theoretical models have been proposed to explain patterns of response to temperatures in marine zooplankton (for review see Dam 2012). A specialist-generalist model predicts a widening of the thermal niche breadth for northern and mid latitude organism that experience greater seasonality (Clarke & 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* reared in our lab, however, was similar among populations. Instead, the fitness pattern observed in this study is more consistent with the third model proposed by Yamahira & Conover (2002). Our results show that northern populations are more sensitive to stressfully high temperatures than their southern counterparts, but are better able to maintain their fitness at lower temperatures. The result is a wholesale shift of all phases of the thermal response of fitness toward lower temperatures 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. The results suggest a tradeoff between fitness effects of low vs. high temperature along the latitudinal cline.

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 non-linear, 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 with decreasing latitude, the latitudinal term used in the model was only marginally significant. A lifetime fecundity of about 120 – 160 nauplii can be expected under optimal thermal conditions for *T. californicus*, assuming food is not a limiting source. Vittor (1971) showed that 300 progeny over a lifetime is achievable. We observed one female producing as many as 579 offspring within her lifetime. Our measure of lifetime fecundity should be an accurate representation of the potential number of offspring produced by *T. californicus* females because they, 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 lab due to the lack of density-dependent factors during our laboratory rearing. For example, inhibition of egg deposition is possible under extreme population densities where pools can reach ~20,000 copepods L⁻¹ during any season except winter (Powlik 1998). However, having high potential lifetime fecundity can be important for successful colonization of unoccupied tidepools where a large initial population size can reduce early extinction risk by buffering against demographic stochasticity.

Our mesocosm 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. Only the shading treatment had a significant effect on fitness in the field experiment. The unshaded, shallow tank treatment had a daily range of 8°C greater than that in the more benign temperatures and ranged from daily highs above 30°C to nightly lows in the teens. In the lab, we observed reductions in fitness at

constant temperatures above around 23°C. Acute lethal temperatures for *T. californicus* are typically around 38°C (Kontogiannis 1975, Willett 2010). This result indicates that the time frame of thermal variability is important to the fitness consequences. Copepods survived and thrived under regular exposure to a few hours of stressfully warm temperatures. Physiological mechanisms for coping with brief periods of thermal stress may therefore be enough to maintain fitness with high-frequency daily cycles that include temperatures near the lethal limits.

We found the lowest population growth in several populations in the unshaded deep treatment, which had the highest daily mean temperature but a daily range that was around 7°C lower than the shaded deep tank. The difference in daily mean among treatments was remarkably small. The shaded treatment was only around 1°C cooler than the unshaded, and the unshaded deep was <1°C warmer on average than the shallow. However, the difference in daily maximum was greater among treatments (Fig. 3C). This result also indicates that fitness of copepods may integrate over high frequency thermal variation, but be more sensitive to small changes in the mean.

In summary, our results indicate two main life history tradeoffs 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. Finally, the field 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, indicating that daily temperature fluctuations have smaller effects on fitness than consistently elevated temperatures.

Our results indicate that a suite of life history traits show shifts in their temperature response with latitude, and that high latitude populations do not show indications of broader thermal niches despite living in more seasonally variable environments.

Figures

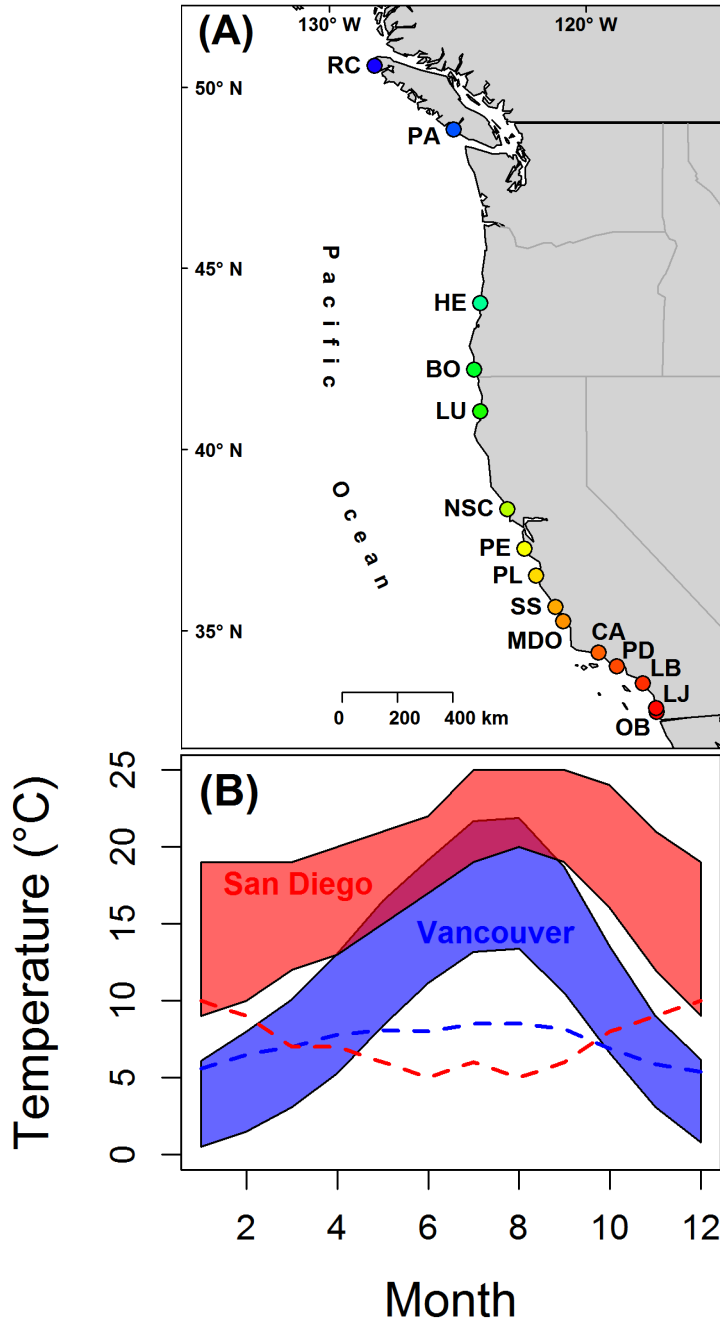


Figure 1. Sampling locations of *T. californicus* populations (A): Raft Cove, BC (RC) 50°58' N, 128°23' W; Pachena, BC (PA) 48°83' N, 125°15' W; Heceta, OR (HE) 44°03' N, 124°13' W; Boardman, OR (BO) 42°02' N, 124°36' W; Luffenholtz, CA (LU) 41°04' N, 124°12' W; North Salmon Creek, CA (NSC) 38°35' N, 123°07' W; Pescadero, CA (PE) 37°26' N, 122°04' W; Point Lobos, CA (PL) 36°51' N, 121°95' W; San Simeon, CA (SS) 35°64' N, 121°19' W; Montaña de Oro, CA (MDO) 35°25' N, 120°89' W; Laguna Beach, CA (LB) 33°54' N, 117°78' W; La Jolla Cove, CA (LJ) 32°85' N, 117°27' W; Ocean Beach, CA (OB) 32°75' N, 117°25' W. Recorded monthly air temperature between Vancouver, shown in blue, and San Diego, shown in red (B). Bands indicate daily high and low temperatures. The difference between these highs and lows are represented by dashed lines as the daily range.

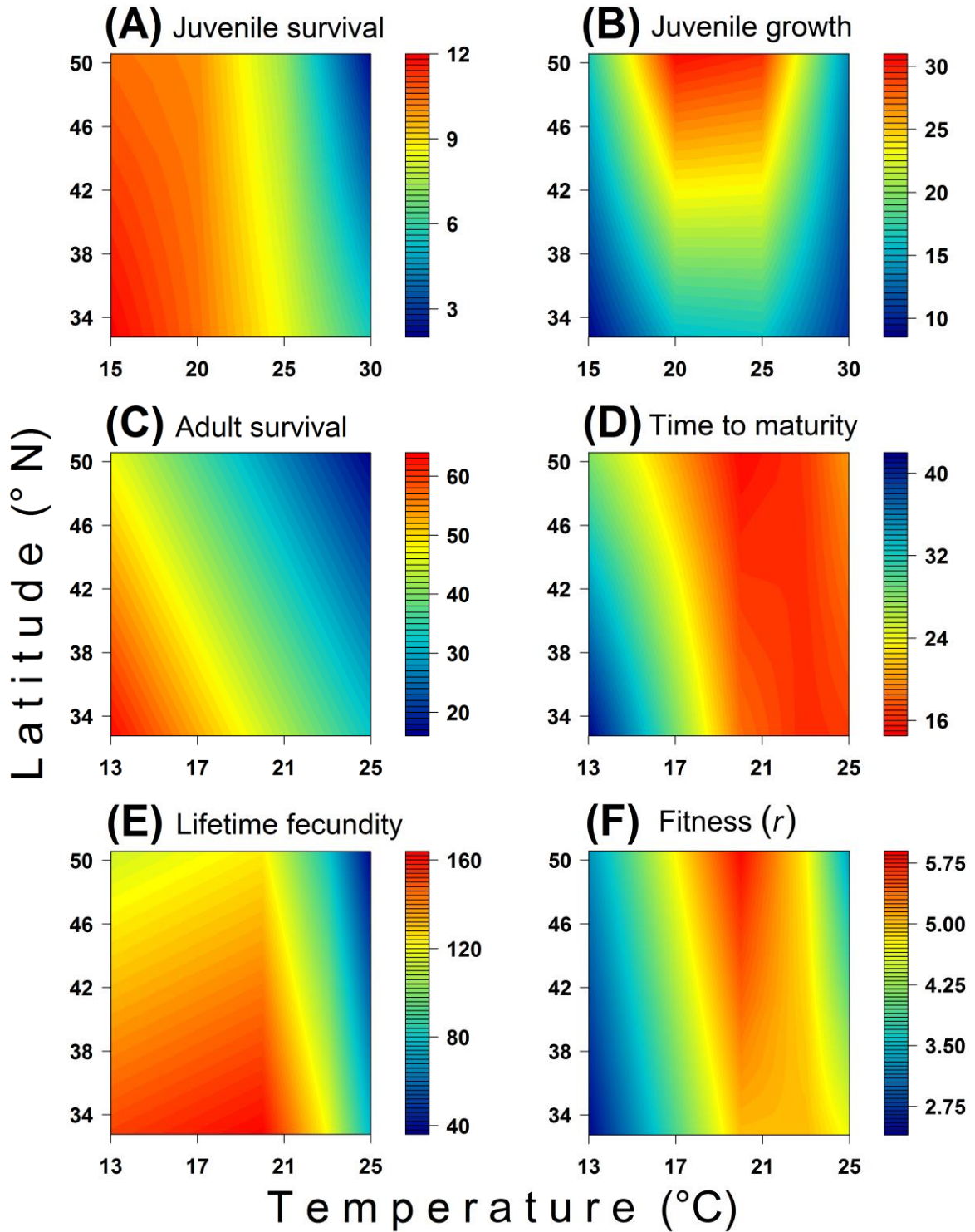


Figure 2. Heat maps of juvenile survival (days) (A) and growth ($\mu\text{m day}^{-1}$) (B), adult survival (days) (C), time to maturity (days) (D), lifetime fecundity (individuals female $^{-1}$) (E), and intrinsic rate of population increase (individuals female $^{-1}$ month $^{-1}$) (F). Trait values, shown on the color scale, were predicted as a function of temperature and latitude using model terms listed in table 1.

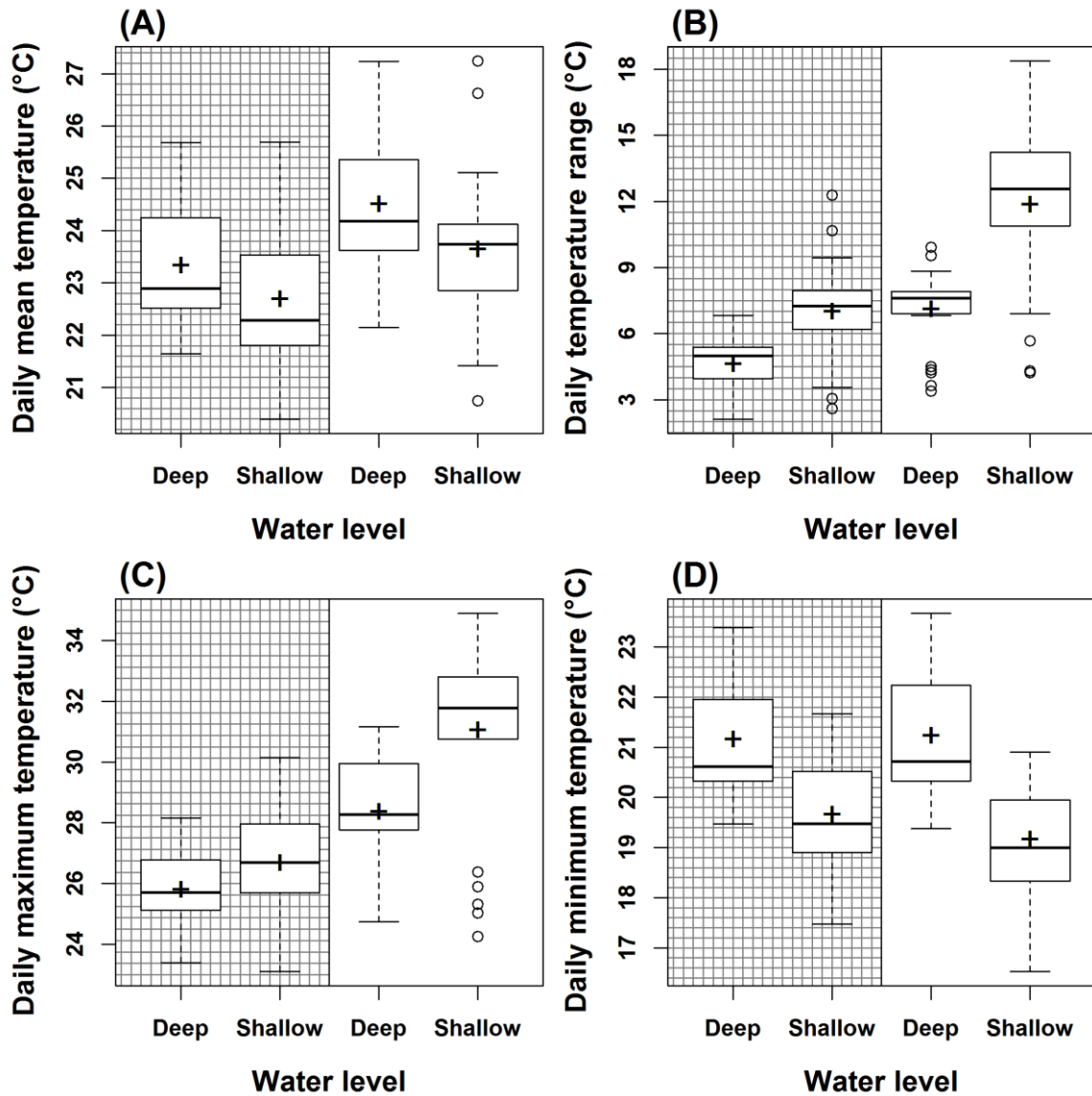


Figure 3. Boxplots showing the median, quartiles, and whiskers showing 1.5 times interquartile range of daily temperature mean (A), range (B), maximum (C), and minimum (D) under experimental mesocosms with different water depth and shading combinations. Boxplots in cross-hatched and white regions are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

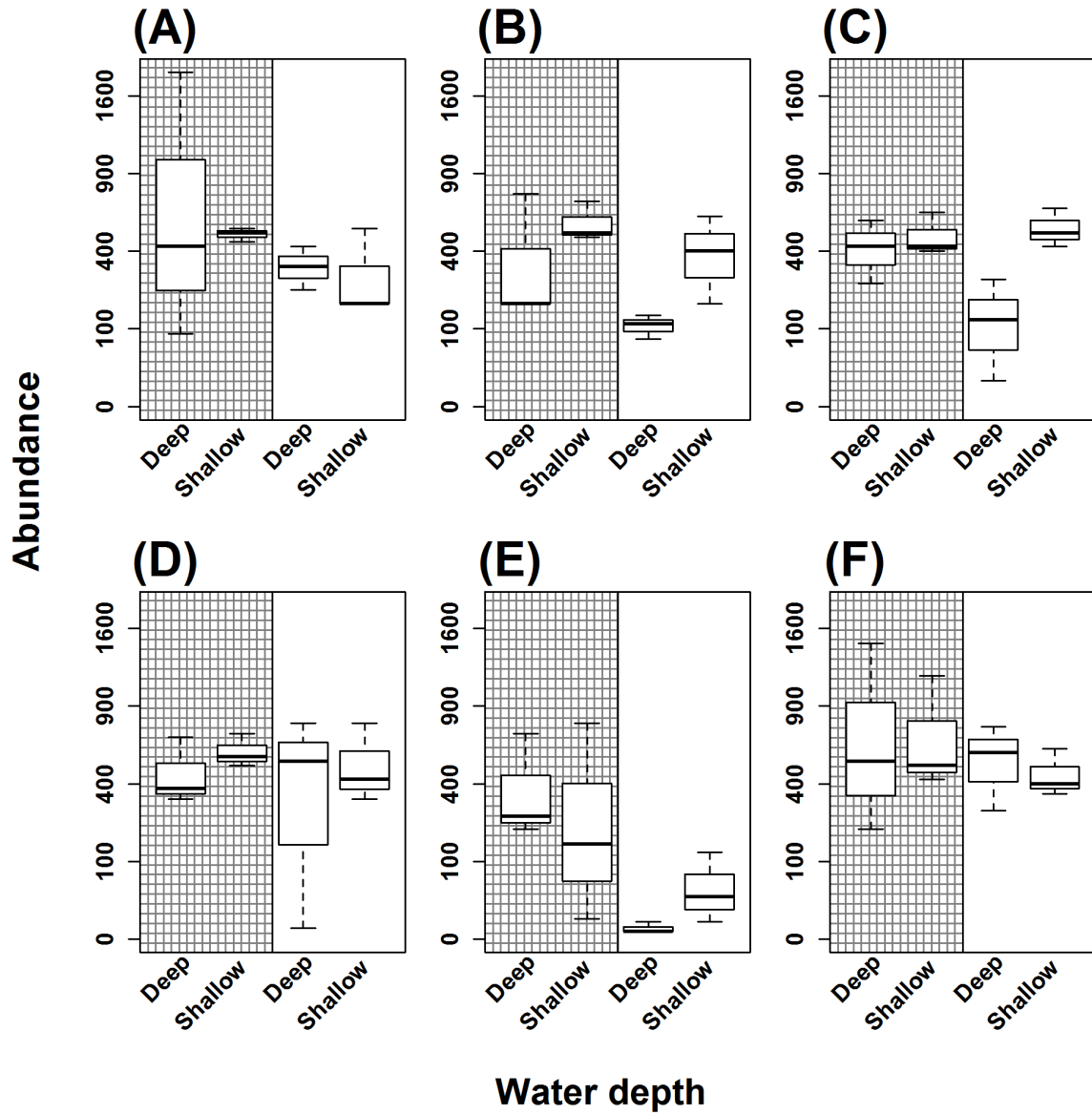


Figure 4. Boxplots showing the median, minimum, maximum, and quartiles of abundance for northern (A-C) and southern (D-F) *T. californicus* populations after 7 weeks in experimental mesocosms with different water depth and shading combinations. The populations used are as follows: RC (A), PA (B), HE (C), PL (D), SS (E), and OB (F). Boxplots in cross-hatched and white regions are shaded and unshaded treatments, respectively.

Tables

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 -value
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
	R^2	0.421	-	-	-
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
	R^2	0.382	-	-	-
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	<0.001
	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	0.233
	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	0.081
	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:

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

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

Effect	df	SS	MS	<i>F</i>	<i>p</i> -value
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 x Depth	5	236.0	47.2	0.924	0.474
Pop x Shading	5	189.7	37.9	0.742	0.596
Depth x Shading	1	71.8	71.8	1.404	0.242
Pop x Depth x Shading	5	97.5	19.5	0.382	0.859
Residual	48	2453.0	51.1	-	-

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

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