FREQUENCY OF SUBLETHAL THERMAL STRESS EVENTS DETERMINES TOLERANCE TO SUBSEQUENT HIGH TEMPERATURE CHALLENGES IN CALIFORNIA MUSSELS

A THESIS

Presented to the Department of Biological Sciences

California State University, Long Beach

In Partial Fulfillment

of the Requirements for the Degree

Master of Science in Biology

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December 2017

ProQuest Number: 10638620

ProQuest 10638620

ABSTRACT

FREQUENCY OF SUBLETHAL THERMAL STRESS EVENTS DETERMINES

TOLERANCE TO SUBSEQUENT HIGH TEMPERATURE CHALLENGES

IN CALIFORNIA MUSSELS

By

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December 2017

Climate change models predict increased frequency and intensity of extreme thermal events, suggesting that exposure to stressful high temperatures will likely become more common for many organisms. I investigated how frequency of exposure to sublethal temperature stress impacted the relative shell growth and size-specific tissue mass of the California mussel, *Mytilus californianus*. Mussels were exposed in the lab to 32 °C during simulated low tides 0, 1, 4, or 7 days per week for 8 weeks or transplanted into rocky intertidal plots exhibiting a range of thermal conditions in the field for 12 weeks, then challenged with repeated exposures to a more extreme temperature (36, 39, or 42 °C) for 5 sequential days. As predicted by theory, increased frequency of exposure to sublethal heat stress invoked a cost to individuals, expressed as reduced shell growth or size-specific tissue mass, but also resulted in higher survival following subsequent exposure to potentially lethal temperatures.

Keywords: climate change, heat stress, growth, survival, trade-off, intertidal zone

ACKNOWLEDGEMENTS

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CHAPTER 1

INTRODUCTION

Global average temperatures are increasing rapidly and are expected to continue to do so for the foreseeable future (Hayhoe et al., 2004; Intergovernmental Panel on Climate Change [IPCC], 2014). The intensity and frequency of extreme thermal events, typically defined as the outermost 10% of a given distribution, are also expected to increase (Moser et al., 2009; Hobday and Pecl, 2014). As a consequence, exposure to stressful temperatures will likely become more common in the future for many organisms (Easterling et al., 2000; Bell et al., 2004; Swain et al., 2016). Biological consequences of increasing temperature have already been observed: distributions of many species have begun to shift poleward (Barry et al., 1995; Parmesan and Yohe, 2003; Sorte et al., 2010) and major alterations in population dynamics and community structure are consistent with predicted effects of climate change (Sala et al., 2000; Thomas et al., 2004). Knowledge of how key organisms will likely respond to the complex challenges of climate change will be crucial to understanding how important ecosystem processes and functions may change, determining the success of future conservation and resource management efforts (Hooper et al., 2005; Cheung et al., 2009).

Acute (relatively short-term) exposure to high temperatures often directly precedes mass mortality events in natural populations (Garrabou et al., 2009; Jones et al., 2009; Marbà and Duarte, 2010). Conversely, chronic (prolonged or repeated) exposures to sublethal yet stressful temperatures can to lead to acclimation, physiological changes that can increase an individual's tolerance to a more extreme future environmental challenge (Somero, 2002). Many organisms defend against stressful environmental conditions by exhibiting a characteristic "heat shock response," preferentially synthesizing a variety of proteins that refold denatured proteins

(Roberts et al., 1997; Tomanek and Somero, 1999), dismantle irrevocably damaged proteins (Hofmann and Somero, 1995), and defend against radical oxygen species (Lesser et al., 2010; Tomanek and Zuzow, 2010). Previous exposure to warmer temperatures has been shown to increase both the onset temperature of an organism's induced heat shock response and the temperature at which the response is maximal (Tomanek and Somero, 1999; Buckley et al., 2001). By preventing the aggregation of damaged proteins and facilitating their renaturation, the heat shock response can play a particularly important role in the acclimation of organisms to more stressful thermal conditions (Parsell and Lindquist, 1993).

Organisms living near the boundaries of their distributions may live very close to their thermal tolerance limits, with associated constraints on their potential capacity for acclimation to higher temperatures (Helmuth et al., 2002; Somero, 2010). Stillman (2003) demonstrated that prior exposure to elevated temperature led to increases in both upper and lower thermal limits of cardiac function of four congeneric species of porcelain crabs. Yet the upper thermal limits of the two warmer-adapted and more heat-tolerant species did not increase nearly as much as did the limits of the cooler-adapted species. More generally, although lower thermal limits appear to be quite plastic, upper thermal limits are often highly conserved across taxa and largely fixed, creating a physiological barrier that may constrain potential acclimation to higher temperatures (Stillman, 2003; Araujo et al., 2013). Increased environmental variability can lead to an increase in the maximum temperature to which organisms are exposed, increasing the risk that species' tolerance limits will be exceeded (Gaines and Denny, 1993; Martin and Huey, 2008). Maximum, rather than average, environmental conditions are often what determine the risks of physiological stress or mortality to individuals (Denny, 1995; Gedan et al., 2011), and even short-term

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exposure to temperatures that exceed organisms' thermal tolerance limits can result in high mortality rates within a population (Harley, 2008).

For individuals that are capable of thermal acclimation, activation of the heat shock response may require a significant energetic investment (Hawkins, 1991), imposing trade-offs between survival and other life history traits (Krebs and Loeschcke, 1994; Somero, 2002; Petes et al., 2008). Life history theory predicts that an increase in the proportion of energetic resources allocated to one physiological process necessarily decreases the available energy to be invested elsewhere (Stearns, 1992). Elevated temperature stress that stimulates the heat shock response is associated with higher metabolic rates (Roberts et al., 1997; Somero, 2002). Energy invested in these activities may explain observed reductions in individual growth rates (Schneider et al., 2010). For this reason, individual growth has been identified as a simple indicator of potentially important impacts of environmental stress over time and space (Widdows et al., 2002; Dahlhoff, 2004). Current theory suggests that if resources increase or the relative energetic cost of thermal defense decreases, then an individual's investment in defense will increase (Tuomi et al., 1983; Cohen and Mangel, 1999), a prediction that has been supported by experimental data (e.g., Fitzgerald-DeHoog et al., 2012). The potential effects of increasing frequency of sublethal temperature exposure on the heat shock response are less clear. Cohen and Mangel's (1999) model also predicts that as the probability of an extreme stress event increases, investment into defense against the stress will increase up to a critical level. Above that level, it is presumably no longer cost effective to build defenses, and relative energetic investment is predicted to taper off or even decrease. However, other models (e.g., Poitrineau et al., 2004) suggest that when the frequency of stress events is high, selection may favor increased investment in a constitutive (always available) defense.

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Regardless of the initial level of defense deployed by an individual, a related question is whether responding to multiple consecutive challenges sets a limit to the potential for acclimation to buffer an organism from the negative effects of exposure to high temperatures. As temperature variability is predicted to increase in many regions of the globe, exposure to stressful temperatures will likely become more common or prolonged for many organisms. Although there is no currently recognized universal definition of a "heat wave," many scientists use three to five days of unusually high maximum (and sometimes also minimum) temperatures in a given area (e.g., Pezza et al., 2012). To date, the physiological capacity of individuals to withstand such repeated stressful exposures has not been explored in great detail. The cumulative effects of multi-day stress events may overwhelm whatever prior physiological acclimation might have occurred, such that individuals that survived the initial event may still eventually die after the second, third, or fourth exposure.

Due to daily variation in tidal height, the rocky intertidal zone is regularly subjected to both aquatic and aerial conditions, and has long been considered a "natural laboratory" for investigating ecological patterns in relation to local environmental conditions (Connell, 1972; Somero, 2002). Organisms in rocky intertidal systems experience extremely high levels of environmental variability over relatively small spatial and temporal scales (Denny, 1995; Denny, 2006), allowing this habitat to serve both as an early warning system and predictive tool for the impacts of climate change (Barry et al., 1995; Sagarin et al., 1999; Helmuth et al., 2006). Given its inherent variation in temperature (Somero, 2002; Denny et al., 2011), the rocky intertidal zone is an ideal system to examine how thermal history influences potential trade-offs between survival and other demographic traits. This is particularly true for ectotherms that cannot physiologically regulate their body temperature (T_b), such that T_b's are tightly linked to local

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environmental conditions (Huey and Kingsolver, 1989; Martin and Huey, 2008; Angilletta, 2009).

My study focuses on how prior frequency of exposure to sublethal high temperature stress will impact the demographic performance of the California mussel, *Mytilus californianus*, and their capacity to survive multiple consecutive high temperature challenges. *Mytilus californianus* is a characteristic member of rocky intertidal communities along the west coast of North America. The mid-intertidal zone extends from just below average sea level to the upper limit of the average lowest tides; within this zone, mytilid mussels are competitively dominant and are ecologically important as a food source for many species (Paine, 1966; Robles and Desharnais, 2002). Additionally, mytilids act as ecosystem engineers, providing valuable ecosystem functions that include habitat provisioning and nutrient cycling (Borthagaray and Carranza, 2007; Arribas et al., 2014). Sessile benthic organisms such as mussels are attractive candidates for studies examining thermal stress effects because they cannot behaviorally mitigate environmental temperatures (except for minor adjustments in gape and orientation) and must instead rely primarily on physiological defenses (Roberts et al., 1997; Harley, 2008). *Mytilus californianus* exhibits a high degree of plasticity both survival and growth in response to variation in temperature (Dahlhoff and Menge, 1996; Fitzgerald-DeHoog et al., 2012; Connor and Robles, 2015), making this species a good candidate for investigating life-history trade-offs induced by activation of the heat-shock response and the potential limits of such acclimation.

I specifically tested the hypothesis that increasing exposure frequency to high temperature stress would lead to significant reductions in mussel size-specific tissue mass and shell growth under controlled conditions in the lab and when exposed to naturally variable temperature conditions in the rocky intertidal zone. I also tested whether the survival patterns of

these experimental mussels in response to a subsequent series of consecutive high temperature

challenges differed in relation to prior thermal history.

CHAPTER 2

MATERIALS AND METHODS

Collection and Maintenance of Animals

All sampling and field experimentation was done in the mid-rocky intertidal zone at

Abalone Cove Shoreline Park, Rancho Palos Verdes, California (33° 44' 11" N, 118° 22' 12" W)

(Fig. 1). This site is characterized by variable wave exposure and a topographically complex

shoreline typical of many intertidal sites in the Southern California Bight (Ricketts et al., 1985;

Dailey and Reish, 1993). Mussels were haphazardly collected from 1.4 to 1.8 m above mean

lower low water (MLLW), placed in a cooler, and returned to the CSULB marine laboratory for
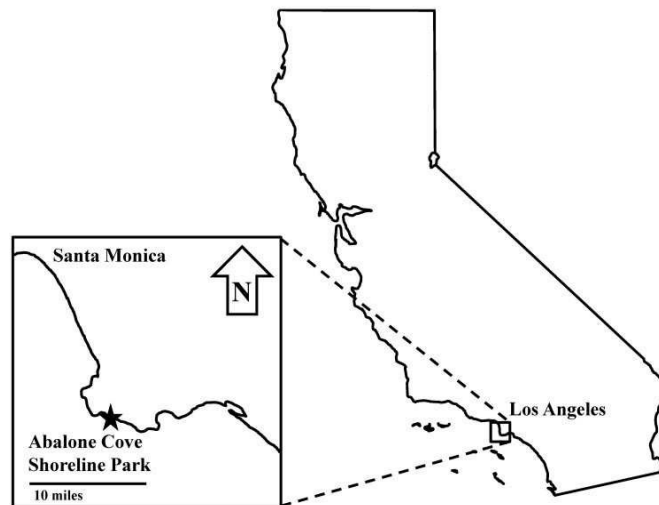
FIGURE 1. Map of California with the location of the field site on the Palos Verdes Peninsula marked in the inset.

processing. The mussels were kept in a recirculating seawater system at 16 °C, exposed to

natural daylight cycles and a daily simulated tidal regime. Experimental mussels were fed a

twice daily ration of cultured marine microalgae consisting of 30% *Isochrysis sp.*, 30%

Thalassiosira weissflogia, 20% *Pavlova sp.*, and 20% *Tetraselmis sp.* (Shellfish Diet; Reed

Mariculture, Campbell, CA), averaging 235 µl of algal concentrate per gram of wet tissue mass.

During each feeding, 30 ml of the cultured microalgae concentrate was added to the approximately 80 L-seawater table, and the mussels allowed to feed for three hours during which water flow was stopped. Air pumps provided aeration for the seawater and kept the phytoplankton in suspension. Over that time interval, mussels were typically able to clear most of the provided food, as assessed visually by changes in water clarity. In principle, algal rations for experimental mussels were within the range of daily chlorophyll values potentially experienced by individuals along the Southern California Bight (Lucas et al., 2011; Fitzgerald-Dehoog et al., 2012). In practice, however, mussels in the lab may have gotten less energy on a daily basis due to the pulsed nature of the feeding regime in the lab, compared to a more constant supply of food in the field.

The mussels used for both the laboratory and field experiments had a mean ± SD shell length of laboratory and field experimental mussels of 3.0 ± 0.3 cm (n = 480) and 2.7 ± 0.4 cm (n = 480), respectively; this small size class of *M. californianus* was chosen for its high growth rate (Coe and Fox, 1942). Individuals were marked using small plastic tags with distinct numeric and color combinations (Brushy Mountain Bee Farm, Moravian Falls, NC), which were attached to the shell with an acrylic adhesive. Mussel shell length was measured to the nearest 0.1 mm with digital calipers, both before and after the experimental period. Mussel shell mass was measured to the nearest 0.01 g after each experimental period as well. Size-specific (relative) mussel growth was calculated as the difference between final and initial shell length, divided by initial length. At the end of each experiment, mussel wet tissue mass was measured to the nearest mg. Size-specific tissue mass (condition) was measured by dividing mussel wet tissue mass by final shell length. Dry tissue mass was not used to calculate condition because many mussel

samples were frozen and stored at -80˚C for future analyses, however wet and dry mussel masses were highly correlated ($n = 288$, $r = 0.83$, p < 0.001).

Laboratory Experiment

Mussels used for the laboratory study were kept in glass dishes (5 cm x 1 cm, diameter x height) on a recirculating seawater table in the CSULB Marine Laboratory from 26 July – 19 October 2014. Mussels were acclimated to the 16˚C water for four weeks (Angilletta, 2009), after which the experiment was run for eight weeks. In order to test how the frequency of thermal stress affects the relative shell growth and size-specific tissue mass of *M. californianus*, tagged individuals were randomly assigned to one of four treatment groups: aerial exposure to sublethal temperature stress 0, 1, 4, or 7 days per week. Mussels were placed in groups of five into small glass dishes to facilitate their removal for exposure to daily stress without damaging their byssal threads ($n = 24$ dishes per treatment). Dish locations on the seawater table were rotated daily to minimize potential location effects through time.

During the experimental period, mussels were exposed to a simulated tidal regime with a daily low tide of six hours' duration. During aerial exposure, mussel dishes were placed into one of 12 experimental chambers (eight dishes per chamber) and mussel temperature was manipulated using computer controlled heat lamps with 250-W ceramic emitters. The control box for each lamp (Herpstat Pro, Spyder Robotics, Rochelle, IL) received input from a dedicated temperature probe inside the associated chamber. The bare end of the probe was placed in the center of the chambers and was comparable in size, color, and temperature to an experimental mussel (based on previous calibrations against live animals). The initial assignment of exposure frequency treatment to experimental chamber was randomized, as was the initial placement of dishes within the chambers. Subsequently, each day I rotated which heating chamber the dishes

were assigned to, as well as their position within the heating chambers. The mussels exposed to a sublethal temperature treatment on a given day were heated to 32˚C, which has been found to elicit a heat stress response in *M. californianus* (Roberts et al., 1997) without significant mortality (Denny et al., 2011; Fitzgerald-Dehoog et al., 2012). Those not receiving a sublethal temperature treatment were still placed in their assigned heating chambers and positions, but were exposed to ambient air temperature during the simulated low tide, which was approximately 18°C. For those receiving the sublethal temperature treatment, I increased the temperature in each chamber (other than the unheated controls) by 8˚C per hour until 32˚C was reached, representative of the rate of temperature change mussels in the field might experience on a hot day (Roberts et al., 1997; Denny et al., 2009). Once 32˚C was reached, it was maintained for four hours, at which point the heat lamps were turned off. Mussel dishes were returned to the seawater table at the end of six hours to recover. Dish locations on the seawater table were rotated daily to minimize potential location effects. For logistical reasons I maintained the same daily schedule throughout the experiment, rather than attempting to mimic the natural local mixed-semidiurnal tidal cycle. Though this experimental design did not explicitly match the timing of local low tides, it does provide some insight into the potential responses of mussels to variation in frequency of prior exposure to sublethal temperature stress.

At the end of the 8-week experimental period, I subjected the mussels to a simulated "heat wave" to test whether the frequency of temperature stress in a mussel's recent thermal history had an effect on the probability of survival when exposed to subsequent repeated high temperature challenges. Each exposure frequency treatment group was partitioned into three peak temperature treatment groups (*n* = 8 dishes per sublethal exposure treatment): 36, 39, or 42 °C temperature challenge per day for 5 days, allowing for a fully factorial design. These specific

temperatures were chosen to represent moderate to severe thermal stress levels potentially experienced by mussels in the field (Denny et al., 2011), and to allow for direct comparison with previous studies (Fitzgerald-DeHoog et al., 2012). The same schedule was followed for both the chronic and subsequent repeated high temperature exposure regimes, differing only in the daily thermal maxima and total time spent at the target temperature (Fig. 2). One mussel was removed from each dish one hour before and after the first thermal challenge was completed, and its gill tissue excised. Shell length, shell mass, gill and body wet tissue mass of these individuals were recorded, and their tissue samples immediately placed in siliconized epitubes and stored at -80°C for potential future analyses of protein content or other biochemical markers. Each morning, 12 hours after each previous high temperature challenge, I assayed post-exposure mussel survival before subjecting the remaining surviving mussels to the next challenge. Gaping mussels that did not respond to their soft tissue being prodded were considered dead, and were removed; I then quantified their final shell length, and tissue and shell mass. After the fifth and final consecutive high temperature challenge, I measured all remaining mussels.
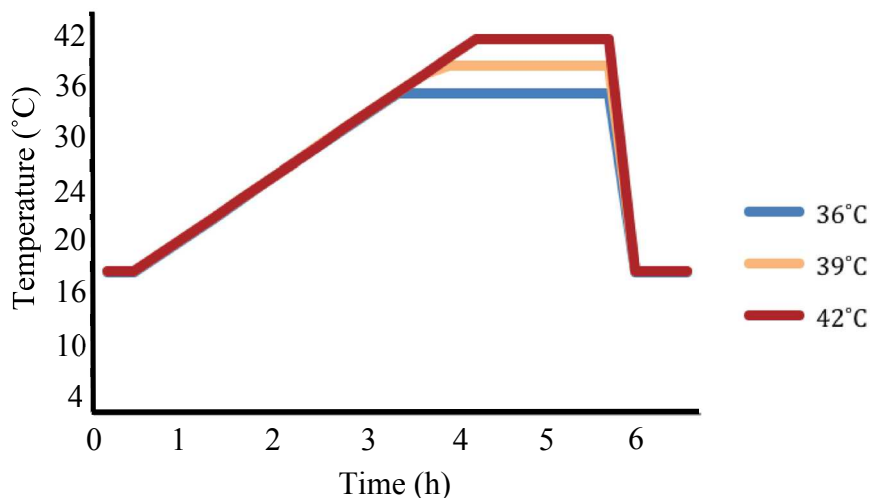
FIGURE 2. Illustration of the temperature stress profiles used. Mussel body temperature was raised from ambient seawater temperature to the target peak temperature at a rate of 8°C h⁻¹. The maximum temperature was held steady until total elapsed time was 6 h.

Field Experiment

Mussels were randomly assigned to one of 24 experimental plots along a horizontal transect 1.3 m above MLLW ($n = 20$ mussels per plot). Plot locations were chosen to represent a range of thermal conditions based on differences in compass orientation, wave exposure, and slope (Harley, 2008; Fitzgerald-Dehoog et al., 2012). Tidal heights were determined with a surveyor's level relative to a benchmark where still tide height had been measured repeatedly (B. Allen, unpublished data). Experimental mussels were placed in their respective plots on 6 July 2015 and to facilitate byssal thread attachment, covered with black plastic mesh (8 mm x 8 mm mesh size) attached to the rock with stainless steel bolts and washers and plastic wall anchors; they were collected and brought back to the lab on 12 October 2015.

Plot temperatures were recorded every 12 minutes to the nearest 0.5˚C with small data loggers (Thermochron iButton, Maxim Integrated Products, Sunnyvale, CA) installed in a spherical brass housing (2.5 cm diameter) painted matte black. iButtons were wrapped in Parafilm (Parafilm M, Pechiny Plastic Packaging, Inc., Chicago, IL) and sealed into a drilled and tapped hole in the housing with silicone (GE Silicone II Kitchen & Bath Caulk, Momentive Performance Materials Inc., NC). The brass housings screwed onto plastic fittings bolted to the substratum. I could not use biomimetic loggers due to the small size of experimental mussels; however, the spherical shape, the thermally absorptive black coloration, and thermally conductive brass material of the housings allow the iButton to provide a standard temperature measure of each plot that is not influenced by the orientation of the sun or housing (Denny et al., 2011). That said, it should be noted that the temperatures of the housings may therefore not exactly match those of the nearby mussels. Temperature loggers were placed in the center of each experimental plot and their data used to build plot-specific thermal histories (e.g., Fig. 3).

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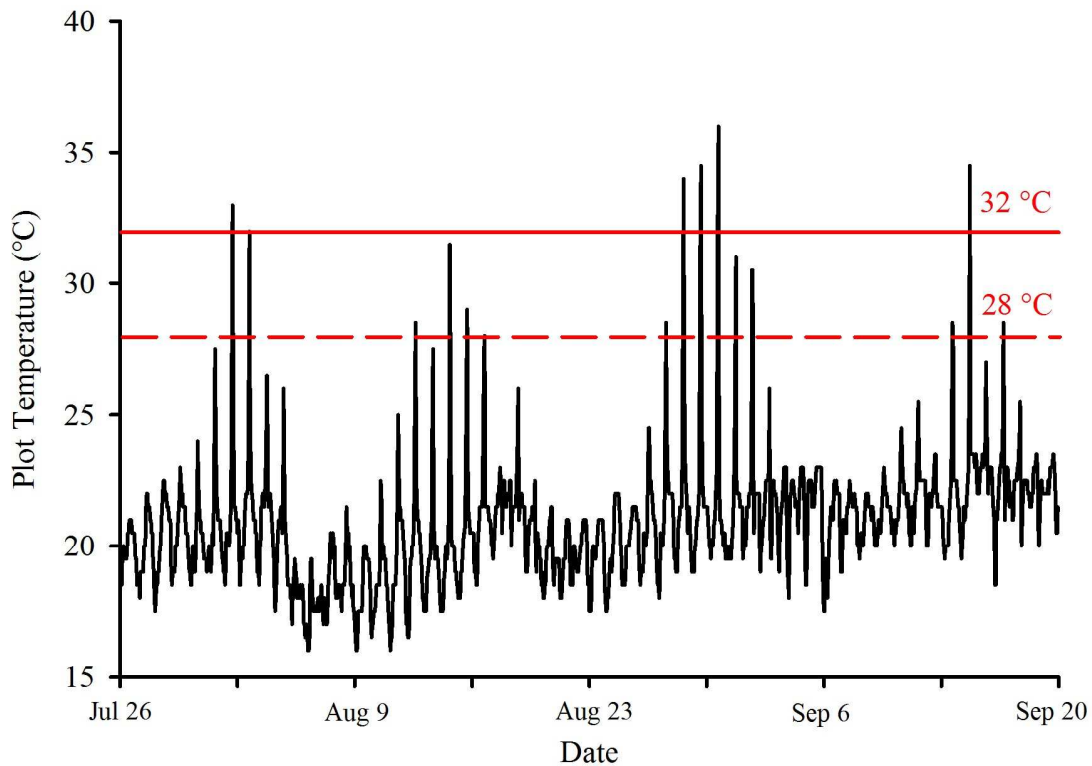
FIGURE 3. Temperature record of an experimental plot in the mid-intertidal zone at Abalone Cove Shoreline Park, Rancho Palos Verdes, CA, from 26 July to 20 September 2015. Red lines denote 28 and 32 ˚C, sublethal thermal stress thresholds for *Mytilus californianus.*

Several temperature metrics were assessed using the temperature data collected from

each plot: the average daily temperature maximum, the average daily temperature range, the

average number of times per week (frequency) experimental plots exceeded 28 and 32˚C, and the

proportion of time plots exceeded 28 and 32˚C over the sampling period (henceforth referred to

as cumulative time above 28/32˚C). Previous research has shown induction of molecular thermal

defenses in California mussels at these temperatures without significant mortality (Roberts et al.,

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1997; Denny et al., 2011; Fitzgerald-Dehoog et al., 2012); I therefore chose 28°C and 32°C as the sublethal temperature stress thresholds.

Fourteen weeks after they were first transplanted, I brought the surviving experimental mussels to the CSULB Marine Laboratory and placed them on the recirculating sea table in the same glass dishes that were used in the laboratory experiment. I partitioned the survivors from each plot into one of four groups: individuals exposed to a peak temperature of 36, 39, or 42°C, or individuals not exposed to any subsequent temperature challenges (pre-exposure control). The shell length and wet tissue mass of the pre-exposure control individuals were recorded immediately and their tissue samples were stored at -80°C for future molecular analyses.

The remaining mussels were subjected to the same experimental conditions during the five consecutive high temperature exposures as in the laboratory experiment. Mussels were placed in groups of five into small glass dishes to facilitate their removal for exposure to daily stress. Each day the mussels were fed a twice-daily ration (once before the simulated low tide and another after) of cultured marine microalgae. During the simulated 6-hour low tide, mussel dishes were placed in heating chambers where their location was rotated daily. The chambers were heated by 8°C per hour using 250-W ceramic emitters until the desired temperature was reached (36, 39, or 42°C) and then shut off at the end of six hours. Each morning after each high temperature exposure I assayed post-stress mussel survival before subjecting the surviving mussels to the next thermal challenge. After the fifth and final high temperature challenge, I collected tissue samples and quantified shell length, and shell and tissue mass of all remaining mussels.

Statistical Analyses

All statistical analyses were done using RStudio 0.98.1091. I checked the data for normality and homogeneity of variances with residuals plots prior to fitting the relevant models. Because individuals within experimental lab dishes ($n = 5$ mussels per dish) or field plots ($n = 20$ mussels per plot) were not independent replicates, mussel growth, condition, and survival were averaged within a dish or plot to avoid pseudoreplication (Hurlbert, 1984).

Analyses of Variance (ANOVAs) were used to quantify the effect of prior frequency of exposure to sublethal temperature stress on the relative shell growth and condition (size-specific tissue mass) of experimental mussels after 8 weeks in the laboratory. Tukey's HSD post hoc tests were used to identify differences among treatment means when the main test was statistically significant. ANOVAs were also used to determine the effect of maximum (peak) exposure temperature on the proportion of mussels surviving after each of five consecutive high temperature challenges. A Wilcoxon signed rank test was performed to compare overall patterns of mussel survival across all five consecutive thermal challenges as a function of peak exposure temperature. A Wilcoxon signed rank test was also performed among mussels exposed to 42°C to examine the effect of prior frequency of exposure to high temperature stress on the proportion of mussels surviving across all five consecutive thermal challenges.

Linear regressions were used to quantify changes in the relative growth and condition of experimental mussels in the field in response to variation in thermal history under natural conditions, using the six calculated temperature stress metrics as the independent variables. ANOVAs were also conducted to determine the effect of peak exposure temperature on the proportion of mussels surviving after each of five consecutive high temperature challenges. A Wilcoxon signed rank test performed to compare overall patterns of mussel survival across all

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five consecutive thermal challenges as a function of peak exposure temperature. Linear regressions were also used to quantify the effects of the six calculated temperature metrics on the proportion of mussels surviving five consecutive exposures to 39˚C (mussels in this treatment group exhibited the most variation in survival in response to multiple thermal challenges).

CHAPTER 3

RESULTS

Lab Experiment

With the exception of one individual that died and was immediately replaced on the second day, there was no mortality during the initial chronic sublethal exposure period. Observed growth rates were generally quite low in experimental mussels; nevertheless, increasing frequency of exposure to sublethal high temperature stress during simulated low tides led to statistically significant reductions in both relative shell growth (Fig. 4a; Table 1) and condition (Fig. 4b; Table 2). Post-hoc tests revealed that mussels exposed once per week did not differ significantly from controls for either shell growth or condition; however, mussels exposed four or more times per week were increasingly negatively affected.
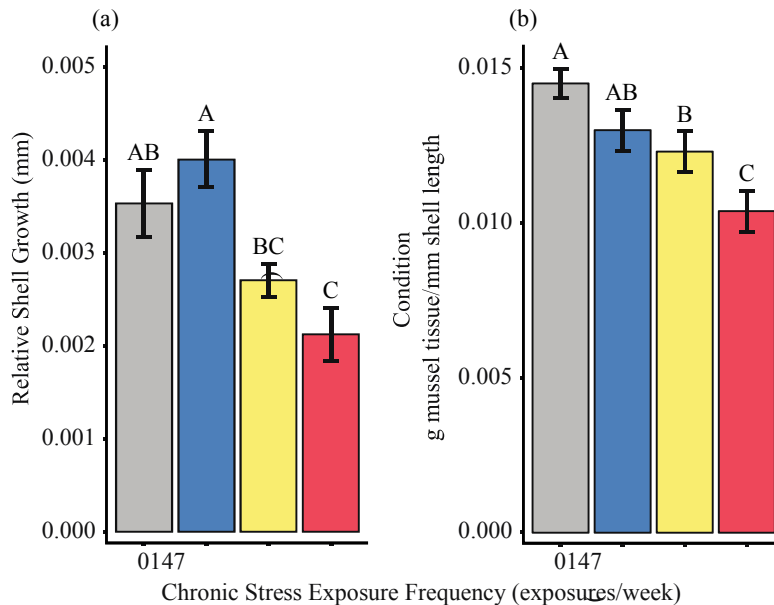
FIGURE 4. Effects of prior frequency of exposure to sublethal high temperature stress on mean (± SE) (a) relative shell growth and (b) condition of *M. californianus* (*n* = 24 replicates per treatment group, 5 mussels per replicate) after eight weeks in the laboratory. Differing letters indicate significant differences among treatments at the α = 0.05 level with Tukey's HSD test following ANOVA.

Comparable results were also observed when mussel condition was estimated using shell mass rather than shell length as a covariate.

TABLE 1. Effects of Prior Frequency of Exposure to Sublethal High Temperature Stress on Relative Shell Growth of Experimental Mussels, After Eight Weeks in the Laboratory (ANOVA)

Source	df	SS	MS	F	P
Exposure Frequency	3	5.07×10^{-5}	1.69×10^{-5}	8.45	< 0.001
Residual	92	1.84×10^{-4}	2.00×10^{-6}	--	--

TABLE 2. Effects of Prior Frequency of Exposure to Sublethal High Temperature Stress on Condition of Experimental Mussels, After Eight Weeks in the Laboratory (ANOVA)

Source	df	SS	MS	F	P
Exposure Frequency	3	2.09×10^{-4}	6.97×10^{-5}	13.50	< 0.001
Residual	92	4.75×10^{-4}	5.17×10^{-6}	--	--

Mussels exposed to 36°C or 39°C exhibited very little mortality over the five consecutive simulated low tides; in contrast, the proportion of mussels surviving following exposure to 42°C was significantly reduced after a single high temperature exposure and continued to decline over the rest of the five-day exposure period (Fig. 5a; Tables 3 and 4). Within the group of mussels consecutively exposed to 42°C, survival patterns differed as a function of prior frequency of exposure to sublethal high temperature stress (Fig. 5b; Table 5). While survival among those previously exposed once or four times per week did not differ significantly from controls over the five consecutive simulated low tides, survival of mussels exposed seven times per week was

significantly different from that of mussels with no prior exposure history. However, by the end of the five-day exposure period, the proportion of mussels surviving did not differ among exposure frequency treatments (Fig. 5b; Table 6).
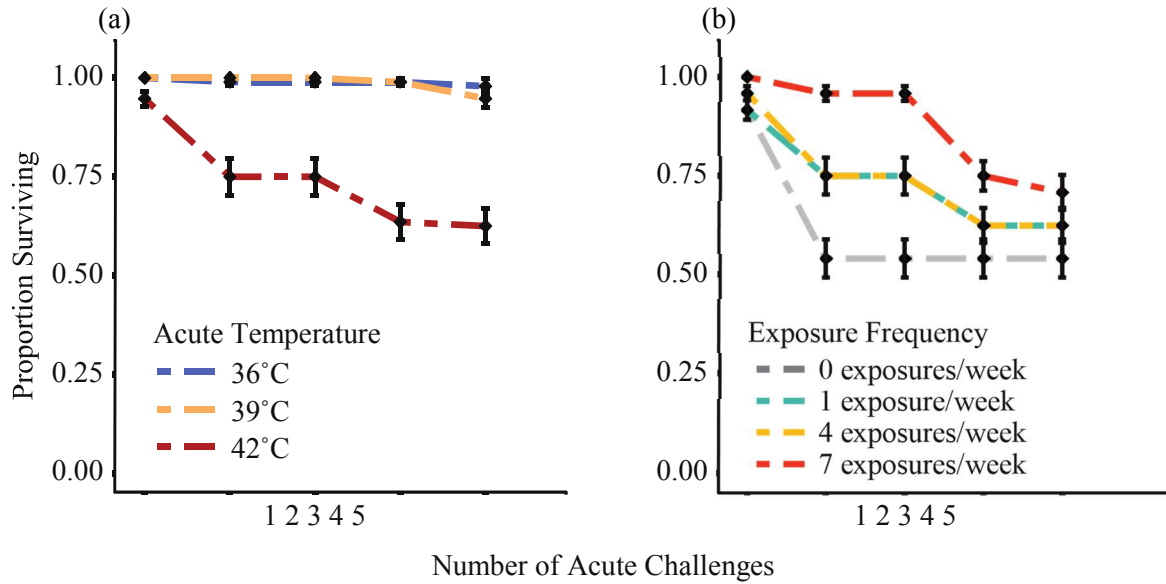
FIGURE 5. Mean (± SE) proportion of mussels surviving five consecutive high temperature challenges, by day, as a function of (a) peak exposure temperature ($n = 32$ replicates per treatment group, 4 mussels per replicate) and (b) among mussels exposed to 42˚C, prior frequency of exposure to sublethal high temperature stress ($n = 8$ replicates per treatment group, 4 mussels per replicate), after eight weeks in the laboratory.

TABLE 3. Effects of Peak Exposure Temperature (39 Versus 42˚C) on the Proportion of Mussels Surviving Consecutive High Temperature Challenges Across Five Days Compared to Individuals Exposed to 36˚C, After Eight Weeks in the Laboratory (Wilcoxon Signed Rank Test)

Source	Coefficient	SE	Z	P
39˚C	-0.0089	0.0592	-0.15	0.880
42˚C	-0.3679	0.0638	-5.76	< 0.001

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TABLE 4. Effects of Peak Exposure Temperature on the Proportion of Mussels Surviving Five Consecutive High Temperature Challenges, by Day, After Eight Weeks in the Laboratory (ANOVA)

Source	df	SS	MS	F	P
Day 1					
Peak Temperature	2	0.06	0.03	5.74	0.005
Residual	93	0.47	0.01	--	--
Day 2					
Peak Temperature	2	0.06	0.03	5.74	0.005
Residual	93	0.47	0.01	--	--
Day 3					
Peak Temperature	2	1.28	0.64	21.46	< 0.001
Residual	93	2.77	0.03	--	--
Day 4					
Peak Temperature	2	1.28	0.64	21.46	< 0.001
Residual	93	2.77	0.03	--	--
Day 5					
Peak Temperature	2	2.46	1.23	32.59	< 0.001
Residual	93	3.51	0.04	--	--

TABLE 5. Effects of Prior Frequency of Exposure to Sublethal High Temperature Stress Among Individuals Exposed to 42°C on the Proportion of Mussels Surviving Consecutive High Temperature Challenges Across Five Days, Compared to Unexposed Controls After Eight Weeks in the Laboratory (Wilcoxon Signed Rank Test)

Source	Coefficient	SE	Z	P
1 Exposure/Week	0.161	0.140	1.15	0.250
4 Exposure/Week	0.180	0.139	1.30	0.195
7 Exposure/Week	0.343	0.136	2.52	0.012

TABLE 6. Effects of Prior Frequency of Exposure to Sublethal High Temperature Stress Among Individuals Exposed to 42˚C on the Proportion of Mussels Surviving Five Consecutive High Temperature Challenges, by Day, After Eight Weeks in the Laboratory (ANOVA)

Source	df	SS	MS	F	P
Day 1					
Exposure Frequency	3	0.04	0.01	0.83	0.490
Residual	28	0.43	0.02	--	--
Day 2					
Exposure Frequency	3	0.04	0.01	0.83	0.490
Residual	28	0.43	0.02	--	--
Day 3					
Exposure Frequency	3	0.69	0.23	3.29	0.035
Residual	28	1.97	0.07	--	--
Day 4					
Exposure Frequency	3	0.69	0.23	3.29	0.035
Residual	28	1.97	0.07	--	--
Day 5					
Exposure Frequency	3	0.11	0.04	0.46	0.716
Residual	28	2.28	0.08	--	--

Field Experiment

Average daily temperature maximum and range, average frequency of exposure to 28 and 32 ˚C, and cumulative time above 28 and 32 ˚C varied across plots, presumably due to differences in wave splash, compass orientation, and slope (e.g., Harley, 2008; Miller et al., 2009; Denny et al., 2011). Mussel loss during the initial exposure period varied among experimental plots in the field, however, it was unlikely due to high temperature stress as average daily maximum temperatures ranged from 22.2 to 28.6 °C. There were, however, multiple large wave events during the study period that produced hydrodynamic forces sufficient to remove several data loggers; mussel losses were greatest after such events, suggesting that

most mortality was due to insufficient byssal thread attachment strength (see also Carrington et al., 2009). I saw no evidence of predation on mussels (i.e., drill holes). Relative shell growth was negatively related to all six temperature metrics; in contrast, mussel condition did not significantly vary in response to any of these variables (Figs 6, 7; Tables 7, 8).

Mussels exposed to 36˚C exhibited no mortality over the five consecutive simulated low tides; in contrast, the proportion of mussels surviving following exposure to 39 or 42˚C was significantly reduced after a single high temperature exposure and continued to decline over the rest of the five-day exposure period (Fig. 8; Tables 9, 10). None of the six plot temperature metrics were significant predictors of the proportion of mussels surviving 5 consecutive exposures to 39˚C (Table 11).
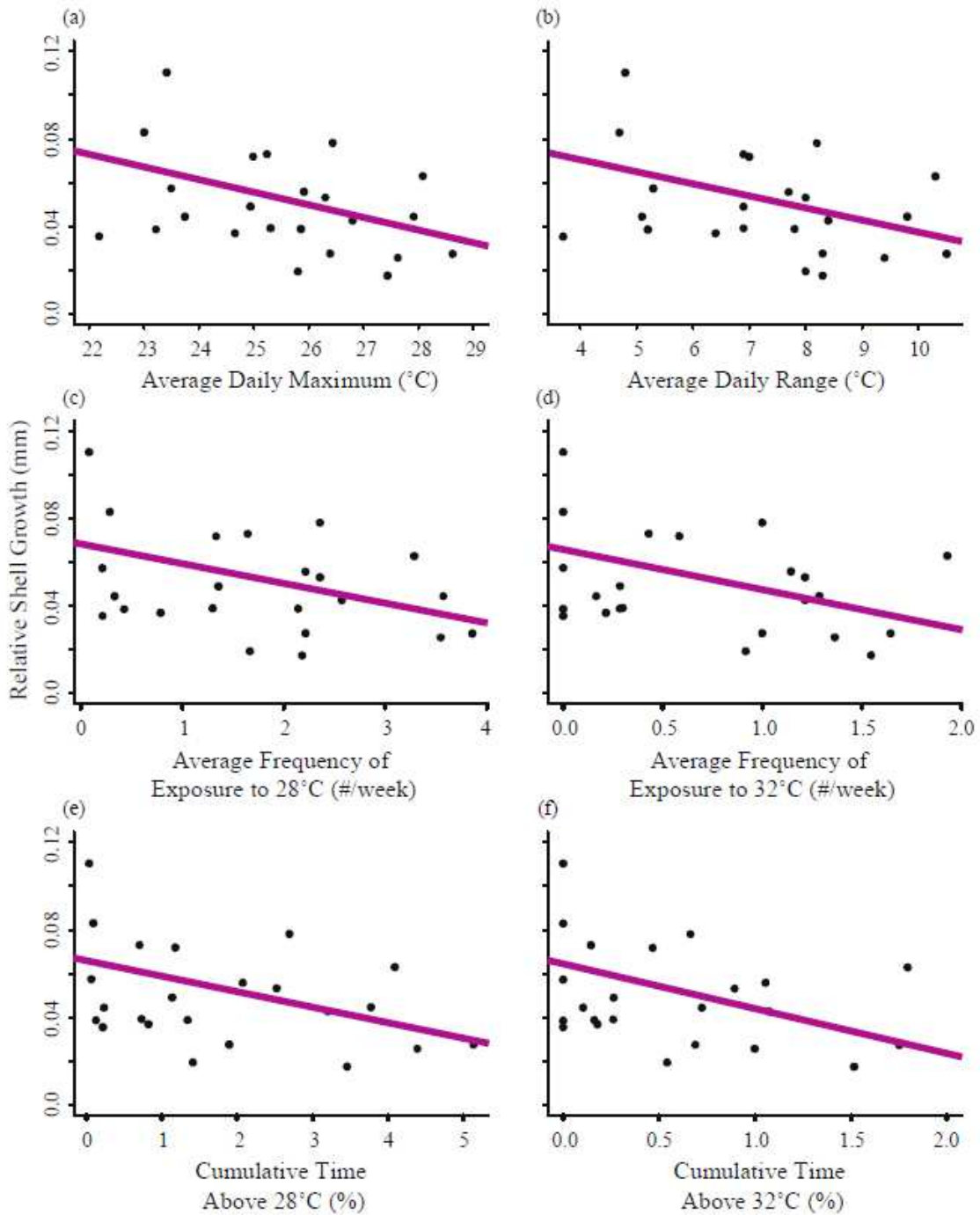
FIGURE 6. Mean relative shell growth of *M. californianus* in the mid-intertidal zone (*n* = 23 plots, 3–17 individuals per plot) as a function of (a) average daily temperature maximum, (b) average daily temperature range, (c) average frequency of exposure to 28°C, (d) average frequency of exposure to 32°C, (e) cumulative time above 28°C, and (f) cumulative time above 32°C. Lines represent the least squares regression equations relating relative shell growth to plot temperature metrics (Table 7).
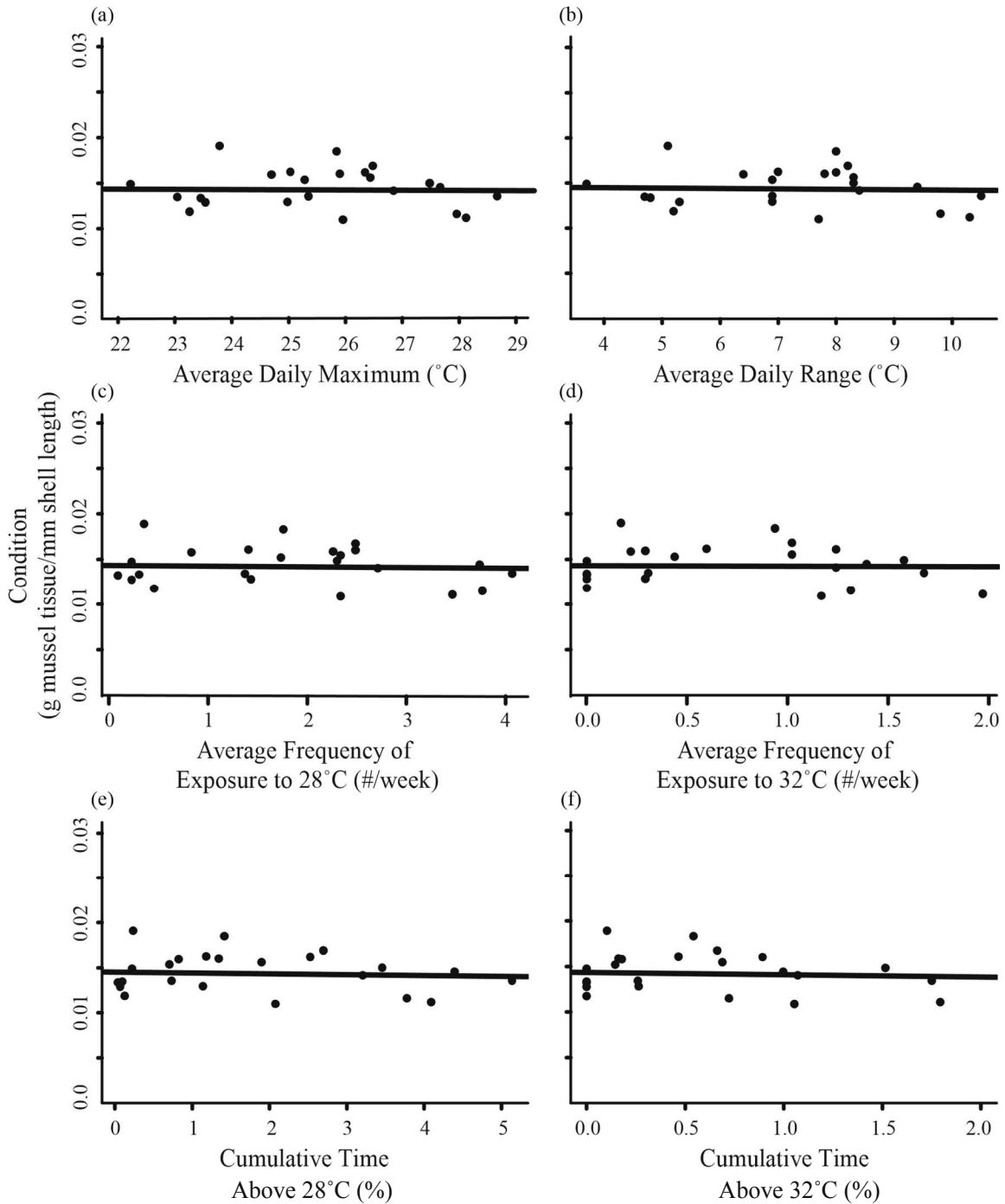
FIGURE 7. Mean condition of *M. californianus* in the mid-intertidal zone (*n* = 23 plots, 3– 17 individuals per plot) as a function of (a) average daily temperature maximum, (b) average daily temperature range, (c) average frequency of exposure to 28˚C, (d) average frequency of exposure to 32˚C, (e) cumulative time above 28˚C, and (f) cumulative time above 32˚C. Lines represent the least squares regression equations relating mussel condition to plot temperature metrics (Table 8).

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TABLE 7. Least Squares Regression Equations Relating Relative Shell Growth of Experimental Mussels in the Field to Plot Temperature Metrics, After 14 Weeks in the Field

Temperature Metric	Intercept	Coefficient	F	P	r^2
Average Daily Maximum	0.200	-0.006	5.53	0.029	0.21
Average Daily Range	0.093	-0.006	5.55	0.028	0.21
Average Frequency of Exposure to 28˚C	0.069	-0.009	5.92	0.024	0.22
Average Frequency of Exposure to 32˚C	0.066	-0.018	5.94	0.024	0.22
Cumulative Time Above 28˚C	0.065	-0.007	6.52	0.023	0.22
Cumulative Time Above 32˚C	0.064	-0.021	6.33	0.020	0.23

TABLE 8. Least Squares Regression Equations Relating Relative Condition of Experimental Mussels in the Field to Plot Temperature Metrics, After 14 Weeks in the Field

Temperature Metrics	Intercept	Coefficient (x1,000)	F	P	r^2
Average Daily Maximum	0.015	-0.02	0.01	0.908	0.001
Average Daily Range	0.015	-0.05	0.04	0.842	0.002
Average Frequency of Exposure to 28˚C	0.015	-0.08	0.07	0.788	0.004
Average Frequency of Exposure to 32˚C	0.015	-0.07	0.01	0.914	0.001
Cumulative Time Above 28˚C	0.015	-0.12	0.24	0.628	0.011
Cumulative Time Above 32˚C	0.015	-0.35	0.26	0.618	0.012
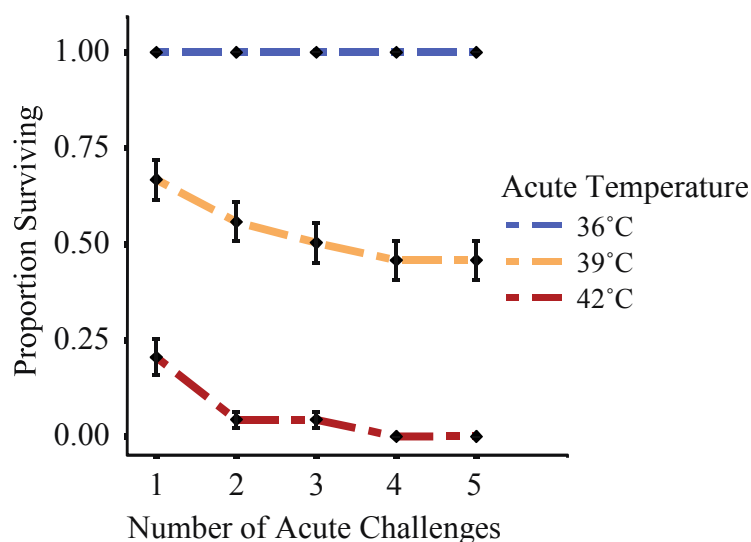
FIGURE 8. Mean (± SE) proportion of mussels surviving five consecutive high temperature challenges, by day, as a function of peak exposure temperature (*n* = 21-23 plots, 4 mussels per plot) after 14 weeks in the field.

TABLE 9. Effects of Peak Exposure Temperature (39 Versus 42˚C) on the Proportion of Mussels Surviving Consecutive High Temperature Challenges Across Five Days Compared to Individuals Exposed to 36˚C, After 14 Weeks in the Field (Wilcoxon Signed Rank Test)

Source	Coefficient	SE	Z	P
39˚C	- 0.7242	0.0973	- 7.44	< 0.001
42˚C	- 2.0186	0.1442	- 13.99	< 0.001

TABLE 10. Effects of Peak Exposure Temperature on the Proportion of Mussels Surviving Five Consecutive High Temperature Challenges, by Day, After 14 Weeks in the Field (ANOVA)

Source	df	SS	MS	F	P
Day 1					
Peak Temperature	2	1.261	0.6307	11.87	< 0.001
Residual	63	3.349	0.0532	--	--
Day 2					
Peak Temperature	2	7.015	3.507	41.63	< 0.001
Residual	63	5.307	0.084	--	--
Day 3					
Peak Temperature	2	10.09	5.047	98.12	< 0.001
Residual	63	3.24	0.051	--	--
Day 4					
Peak Temperature	2	10.044	5.022	97.78	< 0.001
Residual	63	3.236	0.051	--	--
Day 5					
Peak Temperature	2	10.982	5.491	126.2	< 0.001
Residual	63	2.742	0.044	--	--

TABLE 11. Least Squares Regression Equations Relating Among Individuals Exposed to 39°C the Proportion of Mussels Surviving Five Consecutive High Temperature Challenges to Plot Temperature Metrics (Day 5), After 14 Weeks in the Field (ANCOVA)

Temperature Metric	Intercept	Coefficient	F	P	r^2
Average Daily Maximum	0.94	-0.019	0.19	0.670	0.01
Average Daily Range	0.511	-0.007	0.03	0.866	0.01
Average Frequency of Exposure to 28°C	0.486	-0.016	0.10	0.7554	0.01
Average Frequency of Exposure to 32°C	0.483	-0.014	0.04	0.839	0.01
Cumulative Time Above 28°C	0.492	-0.063	0.21	0.653	0.01
Cumulative Time Above 32°C	0.511	-0.074	6.33	0.568	0.02

CHAPTER 4

DISCUSSION

My overall results were consistent with the theoretical prediction that increasing frequency of sublethal environmental stress can result in increased tolerance to more extreme subsequent thermal challenges, but at a physiological cost to individuals – a trade-off. Mussels exposed more often to chronic heat stress in the laboratory exhibited a decrease in relative growth and condition compared to less frequently stressed individuals but were more likely to survive subsequent exposure to more extreme high temperatures. Similarly, intertidal mussels experiencing higher average daily maximum temperatures during aerial exposure in the field grew significantly less than those living in cooler locations on the shore, although they did not differ with respect to condition. I found no support for the idea that there was a threshold frequency of exposure to sublethal stress above which individuals would reduce their investment in thermal defenses (e.g., Cohen and Mangel, 1999); individuals exposed daily to sublethal high temperatures were the most likely to survive subsequent high temperature challenges. The degree to which acclimation can provide an effective defense against high temperature stress does appear to have limits, however, as mussel survival following subsequent more extreme high temperature exposures was negatively related to both peak temperature and number of consecutive exposures. Cumulative effects of multi-day stress events can eventually prove lethal for many individuals, even at lower peak temperatures, as has been found for other species of mussels in the few studies investigating this phenomenon (Jones et al., 2009; Sorte et al., 2011b).

Although there is growing recognition that physiological stress may have important implications for population persistence and species interactions in the face of global climate change, we still lack a general framework for understanding how increasing temperature

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variation will influence organismal responses in natural ecosystems. My results suggest that both the frequency and intensity of stress exposure can affect expression patterns of defensive traits at the individual level, with associated decreases in growth and condition (see also Fitzgerald-Dehoog et al., 2012; Connor and Robles, 2015). Activation of the heat shock response requires energetic investment into several defense pathways associated with protein synthesis and degradation (Martin et al., 1991; Somero, 2002), and the costs may be compounded by reductions in metabolic activity during aerial exposure (Widdows et al., 1979; Widdows and Shick, 1985), which could further reduce the potential scope for growth of intertidal mussels. Responses of mussels in the field to temperature variation did not exactly match those of individuals in the lab. In particular, there was no apparent relationship between frequency of prior exposure to sublethal stress and either individual condition or the proportion of mussels surviving subsequent exposures to a more extreme high temperature. This may be explained in part by the observation that mussels in the intertidal zone did not experience the same range of thermal conditions as was achieved in the lab; for example, the plot that most frequently exceeded 32°C only did so on average 1.93 times per week, versus a maximum of seven exposures per week in the lab. This may be due in part to the timing of my experiment – during the summer, many of the most extreme low tides in southern California occur at night or early in the morning, such that intertidal organisms are covered by water during the hottest part of the day (Helmuth et al., 2002). Repeating the experiment at a different time of year might produce very different results. Additionally, I did not attempt to duplicate the constant feeding conditions available in natural ecosystems (at least during high tide conditions). Given my results, it seems likely that while experimental mussels in the field consumed enough energy to maintain tissue mass and increase in shell length, mussels in the lab were slowly starving in the face of

increasingly frequent thermal stress. Although I designed the feeding regime in the lab using food ration levels that would in theory supply individuals with sufficient energy to support growth, the overall lack of a growth response (and loss of condition) suggests I was not successful. Assuming the experimental mussels in the lab were able to clear most of the provided food during each 3-hour interval, they would have experienced a full stomach twice per day, versus being able to feed more continuously in the field. It's not clear what physiological effects might result from such a different in temporal patterning of ingestion, but it seems likely that some exist. Finally, although most of the experimental mussels should have been prereproductive due to their small size (Suchanek, 1981), some spawning was observed during the initial acclimation period of the laboratory study. No subsequent spawning was observed, however, nor did any of the mussels show appreciable gonad development at the end of the experiment.

It should be noted that observed reductions in mussel condition in the lab were not statistically significant at fewer than four exposures per week, suggesting that condition may be less responsive to temperature effects than growth. The shell growth and tissue growth of mytilid mussels are generally uncoupled, and Hilbish (1989) noted a relatively large or rapid increase in shell length can lead to an apparent reduction in tissue condition. This may explain the apparent (although not statistically significant) decrease in condition in the one exposure per week treatment group. Growth rates in that group were somewhat elevated relative to the control group, perhaps due to positive effects of moderate warming on physiological processes (Miller et al., 2015). If tissue mass did not increase at the same rate, my estimates of condition would decline, even if no actual tissue mass was lost.

The observation from the lab experiment that decreased mussel growth and condition was associated with increased survival is consistent with life history theory that predicts increasing energy allocation demand for one physiological process decreases the amount of energy available for others, leading to negative correlations between phenotypic expression levels of competing traits (Charnov, 1989; Stearns, 1992; Roff, 2000). Not surprisingly, exposure to a higher peak temperature led to higher mussel mortality rates, both after a single exposure and multiple exposures over time. Though my observation of higher levels of mortality at 42°C agrees with observed lethal thermal tolerance limits for *M. californianus* (Denny et al., 2011), my laboratory mussels had generally higher survival rates than expected. Even though the two experiments were done in the same way, it is possible that temporal variation in when the mussels were tested (after eight weeks in the lab versus 12 weeks in the field) or differences in some unmeasured parameter (e.g., relative humidity; Miller et al., 2009) may have been important. Another possibility is that prior exposure to low food stress preconditioned mussels in the lab to be more tolerant of a subsequent thermal stress; similar results have been found for other combinations of stressors (e.g., temperature and heavy metal exposure; Tedengren et al., 2000). However, previous work with food and temperature stress in mussels suggests this is not the case here: proteomics analyses of *M. californianus* exposed to low food conditions found no evidence of elevated expression levels of heat shock and other stress proteins (B. Allen, unpublished data). Nor were those same mussels more resistant to a high temperature challenge than mussels held under high food conditions (Fitzgerald-DeHoog et al., 2012). As the laboratory and field experiments were conducted in different years, I cannot discount the possibility that different environmental conditions played a role in the observed differences in survival patterns;

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for example, there may have been a selection event that occurred prior to my collection of mussel for the laboratory experiment, leaving behind primarily thermo-tolerant individuals.

The fact that mussels generally exhibited increased mortality rates over repeated exposure events is intriguing, as it suggests there are limits to an individual's acclimation potential. Prior exposure to sublethal stress confers some advantage to subsequent high temperature challenges, but the ability to survive one such event does not imply that several comparable events in close succession are equally survivable. This constraint may become more relevant in the future as the frequency and intensity of multi-day extreme weather events increases (Easterling et al., 2000). Such increases could result in further physiological pressure on intertidal organisms and increase the cost of thermal tolerance (Sorte et al., 2011a; Somero, 2012).

Aerobic capacity is thought to be a crucial component in determining the maximum thermal tolerance limits of an organism (Hoppeler and Weibel, 1998; Portner, 2001; Stillman, 2003; Portner et al., 2006; Dowling and Simmons, 2009). During extended periods of emersion, *M. californianus* reduces its metabolic rate and often undergoes anaerobic respiration (Bayne et al., 1976; Widdows et al., 1979). Reduced aerobic capacity limits activation of the heat shock response, so during these time organisms must rely upon prior thermal defense activity (Portner, 2001; Portner, 2002). If exposure to stress increases the oxygen deficit of an individual that must be repaid during the subsequent high tide, physiological limits on aerobic capacity may help explain the observed overwhelming impact of multiple thermal challenges on mussel survival. After several sequential exposures, accumulated damage beyond the ability of the individual to repair before the next stress may eventually lead to mortality. Mass mortality events due to extreme heat waves have already been documented, with bivalves among the most affected taxa

(Smith et al., 2006b; Harley, 2008; Garrabou et al., 2009; Jones et al., 2010). Tsuchiya (1983) recorded a mass die-off of *Mytilus edulis* following just three days of aerial exposures above 40˚C, well within the range of conditions evaluated in this study.

There are likely to be significant ecological consequences of reduced growth, condition, and survival in response to increasing temperature stress on rocky shores. Stress-induced reductions in growth or condition could have population and community level impacts independent of the effects of reduced mussel population abundances. The competitive ability of mussels to maintain dominance is driven by their ability to overgrow competitors and maintain percent cover (Petraitis, 1995; Robles and Desharnais, 2002). Furthermore, mussels move significant amounts of energy from the water column to the benthos and support many organisms at higher trophic levels (Menge, 1992; Ricciardi and Bourget, 1999). Smaller individuals generally allocate fewer resources to reproduction, leading to lower fecundity (Seed & Suchanek, 1992; Olafsson et al., 1994). Slower growth will also reduce the competitive ability of individuals (Petraitis, 1995) and may leave them vulnerable to predators for longer periods of time (Paine, 1976). Larger mussels are less vulnerable to predation (Paine, 1976; Robles et al., 1990) and have greater thermal inertia, potentially making them less vulnerable to thermal stress (Helmuth, 1999; Denny et al., 2011). Given that few species can compete effectively for space in the mid-intertidal zone with *M. californianus* under current conditions, changes in their abundance and biomass may significantly alter local community structure and associated ecosystem functions (Paine, 1966; Blanchette et al., 2006; Denny et al., 2009).

Populations of *M. californianus* along the Southern California Bight have declined significantly since the 1970's in terms of percent cover, bed thickness, and biomass, corresponding with similarly reductions in mussel bed community diversity over that same

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period (Smith et al., 2006a, b). The researchers documenting these patterns could not attribute the mussel losses to habitat destruction, loss of byssal thread complexes, or pollution; rather, they attributed them directly to regional climactic shifts towards warmer sea surface and air temperatures. Of course, declines in one species may facilitate increases in the abundance of others. Warmer-adapted invasive mussel congeners found in more sheltered habitats have shown the potential to outgrow, survive better, and eventually displace their native counterparts as environmental conditions change (Schneider and Helmuth, 2007; Schneider, 2008; Tomanek and Zuzow, 2010; Lockwood and Somero, 2011). Whether such a shift will happen with open-coast species like *M. californianus* remains to be seen.

Understanding the relationship between patterns of organism survival and their local environmental conditions is fundamental to predicting long-term climate change impacts. Our ability to effectively predict the consequences of increasingly common stressors on local community structure and associated ecosystem functions therefore hinges on the development of realistic models of organismal responses to these perturbations, particularly based on experiments done in natural systems. By explicitly partitioning the effects of increasing frequency and intensity of temperature stress on a key rocky intertidal species, this study advances our understanding of the potential for synergistic effects resulting from different aspects of thermal regimes. It also highlights the degree to which environmental challenges can overwhelm the acclimation potential of many individuals, an issue that is likely to become increasingly relevant in the coming decades.

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