Food and Heat Stress in the California Mussel: Evidence for an Energetic Trade-off Between Survival and Growth

LINDSAY FITZGERALD-DEHOOG, JEREMY BROWNING, AND BENGT J. ALLEN*

*Department of Biological Sciences, California State University, Long Beach, 1250 Bellflower Blvd.,
Long Beach, California 90840-3702*

Abstract. In response to thermal stress, many rocky shore organisms exhibit characteristic physiological changes associated with increased tolerance to subsequent high temperatures. Although presumably adaptive, activation of the heat-shock response requires a significant energetic investment and therefore may impose a trade-off between survival and other life-history traits. We investigated the effects of chronic heat stress and variation in food availability on the relative allocation of resources to competing demographic parameters in the California mussel, *Mytilus californianus*. Our data support the idea that acclimatory responses to temperature stress can drive trade-offs among traits, as predicted by theory. Chronic heat stress invoked a cost to individuals, expressed as a reduction in shell growth or size-specific tissue mass in the field and laboratory, respectively. At the same time, prior thermal conditioning resulted in higher proportional survival after acute exposure to more extreme temperatures. Overall, mussels receiving less food exhibited poor condition and survival relative to individuals fed more, suggesting that individuals with limited access to resources are at greater risk because they are less able to mitigate potential costs of thermal stress through physiological mechanisms. Accurately forecasting the effects of climate change in rocky intertidal ecosystems will therefore require understanding not just how organisms respond to different temperature regimes, but also how variation in local resource availability modifies those responses.

Introduction

Anthropogenic global warming is a major driver of current and anticipated changes in population dynamics, species interactions, and community structure from local to global scales (Thomas *et al.*, 2004). In addition to predicting changes in climatic averages, global circulation models also forecast significant increases in the intensity, frequency, and duration of extreme weather events in many parts of the world (Easterling *et al.*, 2000). Increasing temperature variability increases the risk that species' tolerance limits will be exceeded, because even small changes in variance can lead to substantial increases in observed maximum values (Gaines and Denny, 1993). Maximum, rather than average, environmental conditions determine the risk of physiological stress to organisms (Denny *et al.*, 2011), and short-term "acute" exposure to high temperatures can result in very high (*e.g.,* 70%–100%) rates of mortality among affected individuals (Jost and Helmuth, 2007; Harley, 2008; Gedan *et al.*, 2011). In contrast, longer term "chronic" or repeated exposure to sublethal stressful conditions can lead to acclimation and increased tolerance of future extremes (Buckley *et al.*, 2001; Stillman, 2003), complicating our efforts to predict how populations and communities will respond to changing temperatures. Understanding the effects of fluctuating environmental drivers on key demographic parameters (*e.g.,* survival, growth, and reproduction) has therefore been recently recognized as a critical research priority (*e.g.,* Benedetti-Cecchi, 2003; Boyce *et al.*, 2006; Helmuth *et al.*, 2006).

Many organisms respond to environmental stress by preferentially synthesizing molecular chaperones (so-called heat-shock proteins (Hsps)) that stabilize and repair other proteins damaged by high temperatures, osmotic stress, or

low pH (Kültz, 2003). Although this heat-shock response is associated with increased tolerance to subsequent thermal challenges, its activation requires a significant energetic investment in the production of new Hsps and the repair and replacement of damaged proteins (Krebs and Loeschcke, 1994; Somero, 2002). Life-history theory predicts that an increase in resources allocated to one physiological process necessarily decreases the amount available for allocation to others (Stearns, 1992), suggesting that activation of the heat-shock response may impose a trade-off between increased thermal tolerance and other life-history traits (Somero, 2002). Organisms subjected to chronic sublethal temperature stress are expected to exhibit reduced energy storage, growth, or reproduction relative to unstressed individuals, but to have a higher probability of survival after later exposure to even higher extreme temperatures.

For decades the wave-swept rocky intertidal zone has been a model system for the experimental investigation of environmental effects on organismal performance (*e.g.,* Connell, 1961; Dayton, 1971; Menge, 1976; Bertness and Leonard, 1997). The utility of intertidal shores as a natural laboratory is due largely to the severity of the physical environment and the consequent rapid turnover of individuals in the community. Benthic organisms are particularly at risk of physiological stress or mortality from extreme temperatures and desiccation associated with aerial exposure during low tide (Roberts *et al.,* 1997; Harley, 2008; Gedan *et al.*, 2011). Fluctuations in body temperature of 20 °C or more over the course of just a few hours are not uncommon (Denny *et al.*, 2011), and many organisms periodically experience temperatures close to or exceeding their upper thermal limits (*e.g.,* Somero, 2002; Harley, 2008). Coincident with high temperatures, emersed organisms are also at risk of CO_2 accumulation and subsequent acidification of tissues (Allen and Burnett, 2008) and oxidative stress resulting from the production of reactive oxygen species as a by-product of metabolism (Petes *et al.,* 2008). Intertidal invertebrates living higher on the shore or in more wave-protected areas have been found to have higher levels of inducible stress proteins and lower metabolism, growth rates, and reproductive effort compared to individuals in less stressful locations (Bertness and Leonard, 1997; Dahlhoff *et al.*, 2001; Somero, 2002; Petes *et al.*, 2007, 2008), consistent with expectations of an energetic trade-off mediated by activation of the heat-shock response.

Nevertheless, as the authors of these studies are careful to point out, temperature and desiccation stress on rocky shores are typically confounded with food availability. Suspension-feeding organisms living in stressful locations in the intertidal zone experience significantly reduced feeding opportunities due to longer periods of emersion and lower wave splash, while grazers must contend with reduced epilithic microalgal productivity (Dahlhoff and Menge, 1996; Dahlhoff *et al.*, 2001; Denny *et al.*, 2004). This makes it difficult to unequivocally attribute observed reductions in growth or reproduction to costs of activating the heat-shock response, as food limitation would produce the same result. Variation in food availability may also have important implications for the total amount of resources individuals can allocate toward physiological defenses against extreme conditions. Theory suggests that in a heterogeneous environment, investment in survival of unsynchronized stresses should increase if the cost of the defense decreases (Cohen and Mangel, 1999). Increased access to food effectively reduces the marginal cost of allocating energy toward the heat-shock response, because individuals with more resources at their disposal can spend more on defense without having to reduce the amount allocated to competing demographic parameters (Tuomi *et al.*, 1983). In this study, we investigated the effects of chronic heat stress and variation in food availability on the relative allocation of resources to different life-history traits by the California mussel, *Mytilus californianus* Conrad. We used manipulative experiments in the field and laboratory designed to maximize our ability to definitively partition treatment effects between temperature stress, food ration, and their interaction.

On rocky shores along the west coast of North America, *M. californianus* is the dominant competitor for primary space in the mid-intertidal zone and provides structural habitat for many other species (Seed and Suchanek, 1992). Mussels are also an important component in coastal marine food webs. They are a source of strong benthic-pelagic coupling, moving large amounts of energy from the water column to the benthos, and are themselves food for various fishes, sea stars, whelks, and crabs (Seed and Suchanek, 1992). Not surprisingly, changes in the abundance and distribution of *M. californianus* can result in widespread and significant alterations to community structure and function in this ecosystem (*e.g.,* Paine, 1966; Wootton, 1994). Mussels are sessile and must rely on physiological tolerance rather than behavioral avoidance of environmental stress (Menge and Sutherland, 1987). As a consequence, *M. californianus* exhibits a high degree of physiological plasticity in response to variation in both temperature and food availability (Dahlhoff and Menge, 1996; Petes *et al.*, 2008; Menge *et al.*, 2008; Krenz *et al.*, 2011), making this species a good candidate for investigating potential life-history trade-offs induced by activation of the heat-shock response.

Here, we tested the hypothesis that relative to unstressed individuals, mussels exposed to chronic sublethal temperature stress would exhibit a trade-off between thermal tolerance and growth or condition. We examined the relationship between average daily maximum environmental temperatures and mussel growth across a gradient of wave exposure at a single tidal height in the field, complemented by an experiment in which we manipulated food availability and daily temperature stress to mussels under controlled conditions in the laboratory. We then tested whether recent food
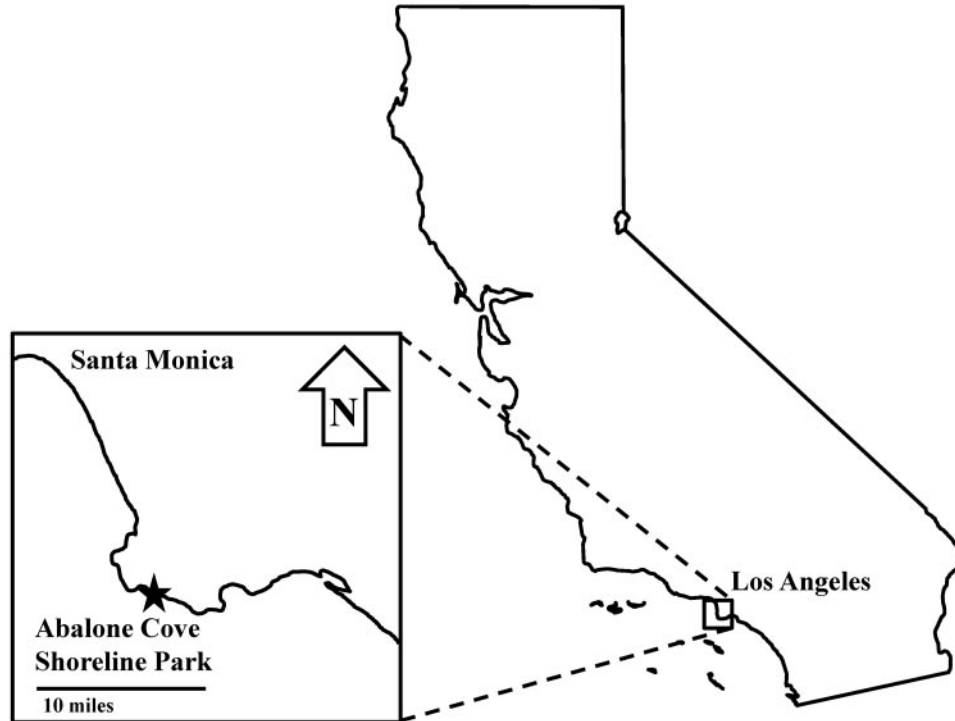
Figure 1. Map of California with the location of the study site on the Palos Verdes Peninsula marked in the inset.

ration or chronic sublethal heat stress influenced the probability of individual survival during a subsequent acute high-temperature challenge. Finally, we investigated how patterns of allocation to thermal defense varied among individuals with differential access to food resources. We predicted that mussels given more food would allocate relatively more resources toward defense, because they would be able to do so without compromising their level of investment in other life-history traits.

Materials and Methods

Collection and maintenance of animals

All sampling and field experimentation was done in the mid-intertidal zone on a rocky headland in Abalone Cove Shoreline Park, Rancho Palos Verdes, California ($33°44'11''$N, $118°22'12''$W) (Fig. 1). This site is characterized by moderate wave exposure and a topographically complex shoreline typical of many intertidal sites on the west coast of North America. Mussels were sampled haphazardly from a height of 1.4 to 1.8 m above mean lower low water (MLLW) on a falling tide, placed in a cooler, and returned to the California State University, Long Beach marine laboratory for processing.

Temperature and mussel growth in the field

To quantify the relationship between temperature and mussel growth in the field, we did a transplant experiment in the fall and winter of 2011–2012. Heat stress during aerial exposure is likely to be particularly important to southern California rocky intertidal organisms during this time of year, as warm sunny days are common and low tides typically occur midday when climatic conditions are most extreme (Helmuth *et al.*, 2002). On 14 October 2011, mussels 2–3 cm in length were collected from a relatively cool wave-splashed location in the field, measured, and marked with small plastic tags bearing unique combinations of color and number (Queen Marking Kit; The Bee Works, Orillia, ON, Canada) attached to their shell with cyanoacrylic adhesive. Mussels were randomly assigned to one of 20 experimental plots along a horizontal transect 1.3 m above MLLW ($n = 20$ mussels per plot). Plot locations were haphazardly chosen to represent a range of thermal conditions based on differences in wave exposure, compass orientation, and slope (Harley, 2008; Denny *et al.*, 2011). Tidal heights were determined with a surveyor's level, relative to a benchmark where still tide height had been measured repeatedly (authors' unpubl. data). Maintaining a constant shore height minimized potential differences in feeding time due to variation in immersion regimes. Mussels were placed ventral side down and covered with plastic mesh bolted to the rock to facilitate byssal thread attachment (after Dahlhoff and Menge, 1996); the mesh was removed after 4 weeks. Relative (size-specific) mussel growth was estimated at the end of 12 weeks as the difference between final

and initial shell length, divided by initial length. Mussel shell length was measured to the nearest 0.1 mm with digital calipers.

Plot-specific temperatures were recorded with small data loggers (Thermochron iButton; Maxim Integrated Products, Sunnyvale, CA), each installed in a spherical brass housing (2.5 cm diameter) painted matte black. iButtons were wrapped in self-sealing film (Parafilm M; Pechiny Plastic Packaging, Inc., Chicago, IL) and sealed into a drilled-and-tapped hole in the housing with silicone caulk; housings were then threaded onto a short polyvinylchloride rod bolted to the substratum (see Denny *et al.*, 2011, for details). The spherical shape of the housing presents the same area for solar heating regardless of the orientation of the mounting, minimizing any effects of differential instrument placement across locations. Temperatures were recorded every 15 min for the duration of the experiment; iButtons have a precision of 0.5 °C and were calibrated prior to deployment to improve accuracy. Although it would have been desirable to use biomimetic loggers that were thermally matched to our experimental mussels, the standard approach of embedding iButtons in silicone caulk within a mussel shell (*e.g.,* Helmuth and Hofmann, 2001; Jost and Helmuth, 2007) would not have worked, given that the minimum mussel length of 7–8 cm required to fit the datalogger was far larger than the 2–3-cm-long individuals we used in our experiment. In practice, the thermal mass of each housing is approximately equal to that of a 7–8-cm mussel (Fitzhenry *et al.*, 2004; Denny *et al.*, 2011). The thermal conditions in each plot were characterized as the 12-week average of the daily maximum temperatures recorded by each logger. This metric provides an integrative measure of chronic high-temperature stress experienced by mussels in each plot during the experiment (Denny *et al.*, 2011).

Food, temperature, and mussel growth in the laboratory

To test the relative effects of food ration and temperature stress on mussel growth, mussels 3–4 cm in length were collected on 01 June 2011, tagged, and acclimated for 4 weeks at 16 °C (ambient water temperature at the collection site) in a 20,000-l recirculating seawater system exposed to natural daylight cycles. Mussels were fed a daily ration of cultured phytoplankton equivalent to the amount given in the "high food" treatment in the experiment detailed below. Following the acclimation period, mussels were randomly assigned to one of four factorial treatment groups: low food ration, low heat stress; low food ration, high heat stress; high food ration, low heat stress; and high food ration, high heat stress. During the following 8 weeks, mussels were kept in 1-l beakers (*n* = 12 beakers per treatment group, 3 mussels per beaker) in a recirculating seawater table. Within each beaker, mussels were placed in a small glass dish (5 cm × 1 cm, diameter × height) to facilitate their removal

for cleaning or exposure to daily temperature stress without damaging their byssal threads. Each beaker was aerated constantly and the water changed several times per day. Beakers were arranged spatially in a randomized complete block design, with 12 blocks total. Block locations on the seawater table were rotated daily to minimize any potential location effects through time.

Food ration was calculated as the daily amount of a concentrated four-species mix of cultured marine microalgae (30% *Isochrysis* sp., 30% *Thalassiosira weissflogia*, 20% *Pavlova* sp., and 20% *Tetraselmis* sp.) added to each beaker (Shellfish Diet; Reed Mariculture, Campbell, CA). Mussels in the high-food treatment groups were given ~185 μl of algal concentrate per gram of wet mussel tissue per day, whereas those in the low-food groups were given ~15 μl g^{-1} d^{-1}. These values were derived empirically from a preliminary study designed to identify ration levels that would support positive mussel shell growth at high food concentrations and zero growth (but no mortality) at low concentrations. Because mussels were capable of clearing their beaker of food within several hours, daily rations were split into three equal portions delivered separately over the course of each day. Mussel wet tissue mass per beaker was estimated from a linear regression of tissue mass on shell length for individuals from the initial collection (wet tissue mass (g) = –1.90 + (0.0879 × shell length (mm)); r^2 = 0.344, $P < 0.001$, $n = 36$); the r^2 value was relatively low due to the small variation in initial shell length. Our experimental food values corresponded to chlorophyll *a* levels of about 148 μg and 12 μg per mussel per day in the high- and low-food groups, respectively. By comparison, nearshore chlorophyll levels in the Southern California Bight can range from 0.5 to 8 μg l^{-1} (Phillips, 2005; Blanchette *et al.*, 2007; Lucas *et al.*, 2011). At the tidal height of plots in the previously described field experiment, mussels at Abalone Cove Shoreline Park are submerged and able to feed for anywhere from 1 to 18 h per day depending on the tidal cycle and local wave conditions, as calculated from historic data available from the U.S. National Ocean Service's Center for Operational Oceanographic Products and Services (NOS, http://tidesandcurrents.noaa.gov) and the U.S. National Data Buoy Center (NDBC, http://www.ndbc.noaa.gov). Assuming a filtration rate of 1 l h^{-1} for mussels of the size we used (Bayne *et al.*, 1976), our experimental food levels spanned the range of daily chlorophyll values potentially experienced by individuals in the field (although the ration in the high-food treatment is likely an overestimate of the amount of chlorophyll *a* assimilated, given that mussels in this treatment group regularly produced pseudofeces).

All experimental mussels were subjected daily to a simulated 6-h low tide. During these periods of emersion, mussels from each beaker (moved as a unit in their glass dish) were assigned to one of 12 blocks on a laboratory bench. As in the seawater table, block locations were rotated

daily to minimize potential location effects through time. Mussels in the high-stress groups were heated to a body temperature of 32 °C under 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 modified to mimic mussel body temperature under that lamp. Probes were embedded in silicone caulk within the shell of a mussel similar in size to the experimental individuals (Helmuth and Hofmann, 2001). Preliminary tests confirmed that probe temperatures were typically within 1–2 °C of the body temperatures of live mussels under the same lamp; we saw no evidence that mussels were using gaping as a mechanism for evaporative cooling (see also Fitzhenry *et al.*, 2004). A heating rate of 8 °C h^{-1} was chosen to be representative of what mussels in the field might experience on a hot day (*e.g.,* Roberts *et al.*, 1997; Denny *et al.*, 2006). Once the target temperature was reached it was maintained for 2.5 h, at which point the heat lamps were turned off. Mussels were returned to their beakers in the seawater table at the end of 6 h to recover. Mussels in the low-stress groups experienced the same emersion regime, but with no additional heating. Unheated ambient air temperatures during emersion were typically 18–20 °C, and relative humidity was 50%–60%.

For logistical reasons, we did not attempt to mimic the natural tidal cycle, but rather maintained the same daily schedule throughout the experiment. Although repeatedly exposing mussels to a single maximum body temperature does not perfectly represent field conditions, our experimental design should give us some insight into how mussels held under different food rations might respond to chronic heat stress. We chose 32 °C as the target body temperature in the high-stress treatments because it is above the threshold that elicits the heat-shock response in *M. californianus* (Roberts *et al.*, 1997) but is not typically lethal (Denny *et al.*, 2011). After 8 weeks, mussel shell length was measured to the nearest 0.1 mm with digital calipers and tissue mass to the nearest 0.1 mg after drying until constant mass at 70 °C.

Acute heat stress and mussel survival

To test whether recent food ration or prior exposure to chronic heat stress had a positive effect on the probability of survival during a subsequent acute extreme temperature event, at the end of the laboratory experiment described above a subset of mussels from each treatment group ($n = 8$ mussels per group, each from a different beaker) were exposed to body temperatures of 36, 39, or 42 °C for a single "low tide" event, and their post-stress survival was quantified. We followed the same heating procedures as in the chronic stress experiment, but with higher peak temperatures. At the end of each trial, mussels were placed back in the seawater table to recover, and their status was assessed

after 24 h; mussels that gaped maximally and did not respond to prodding or squeezing of their valves both in and out of water were scored as "dead." Mussels that closed easily or exhibited only slight gaping were scored as "alive." We did the trials on three days with one peak temperature per day, challenging each mussel only once. We recognize that this experimental design confounds peak temperature with time, limiting our ability to make inferences about differences in survival across temperatures ("pseudoreplication" *sensu* Hurlbert, 1984). It does, however, provide greater statistical power to detect differences among treatment groups, which was our primary question of interest.

Statistical analyses

We tested the relationship between relative mussel growth and average daily maximum temperature in the field with simple linear regression. Mussel growth was compared among treatments in the laboratory experiment with a general linear model that included block as a random nuisance factor, initial shell length as a covariate, food ration and heat stress as fixed main effects, and their interaction. Size-specific mussel dry tissue mass was compared with a similar model, but with final shell length as the covariate. Beakers were used as the error component in both models (Winer *et al.*, 1991). Visual inspection of residuals was done for every analysis, and the assumption of homogeneity of slopes was checked prior to fitting relevant models. Where variances showed significant heterogeneity or departures from normality were detected (*e.g.,* mussel shell length and tissue mass), the data were transformed using a $\ln(x + 1)$ function. Tukey's HSD *post hoc* tests were used to identify differences among appropriate means when the main test was statistically significant. Differences in mussel survival frequencies among treatments, holding temperature constant, were assessed with the Cochran-Mantel-Haenszel (CMH) statistic. We did not formally test for differences among temperatures given the limitations of the experimental design. All statistical analyses were done with SAS software, ver. 9.3 (SAS Institute, Inc., Cary, NC).

Results

Temperature and mussel growth in the field

At a single tidal height in the field, daily maximum plot temperatures varied substantially, even among locations at small spatial scales, due to differences in wave splash, compass orientation, and slope (see also Harley, 2008; Denny *et al.*, 2011). During the study, the dataloggers recorded average daily maximum temperatures ranging from 18.7 to 27.5 °C and absolute maximum temperatures from 29.0 to 45.0 °C; the two measures were highly correlated across plots ($r = 0.92$, $P < 0.001$, $n = 18$). Across the
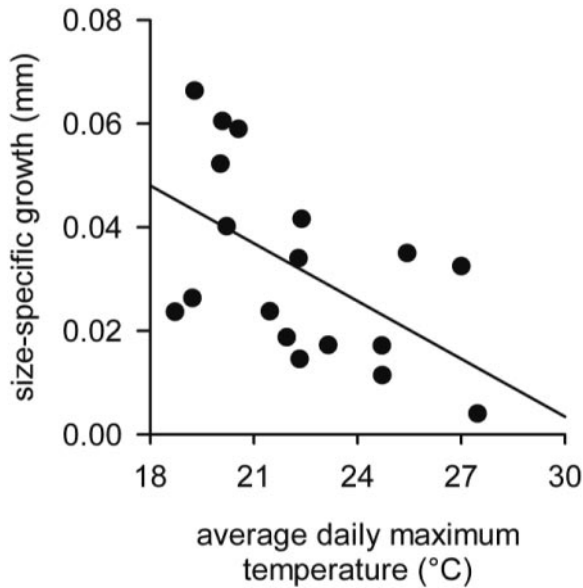
Figure 2. Mean size-specific growth of the California mussel, *Mytilus californianus,* in the mid-intertidal zone ($n = 1$–16 individuals per plot) as a function of local plot temperatures (average daily maximum; 15 October 2011–14 January 2012). Size-specific growth was calculated for each mussel as change in shell length/initial shell length. The line represents the least squares regression equation: growth = 0.115 – (0.004 × temperature), $P = 0.019$, $r^2 = 0.30$, $n = 18$ plots.

horizontal transect, mean size-specific mussel shell growth within plots was negatively related to average daily maximum plot temperature, a pattern that was statistically significant (growth = 0.115 – (0.004 × temperature); $P = 0.019$, $r^2 = 0.30$, $n = 18$; Fig. 2). Loggers in the hottest locations along the gradient of wave exposure recorded temperatures higher than 30 °C on 29 days, whereas maximum temperatures recorded in the coolest locations were lower than 30 °C over the entire experimental period. Synthesis of Hsps is induced in *Mytilus californianus* after exposure to temperatures ranging from 15 to 30 °C, depending upon prior thermal history (Roberts *et al.*, 1997; Halpin *et al.*, 2004), suggesting that the reductions in mussel growth we observed in the hotter plots likely occurred concurrently with induction of the heat-shock response. Although we were able to recover the majority of transplanted mussels in most plots, two plots had no mussels remaining and several plots had only a few individuals. There was a relatively large wave event at Abalone Cove Shoreline Park in the days immediately following the removal of protective plastic mesh from the mussels at the one-month mark. Most of the missing individuals were gone immediately thereafter, suggesting that the strength of their byssal thread attachment was insufficient to withstand the resulting hydrodynamic forces. Other than a few instances of whelk predation (indicated by drill holes), survival was close to 100% during the rest of experiment.

Food, temperature, and mussel growth in the laboratory

With the exception of two individuals that died near the beginning, there was no mortality during the 8-week laboratory experiment; however, most mussels did not increase in shell length. We observed measurable shell growth in mussels of this size in a preliminary experiment, so the lack of growth this time was surprising as the only difference in protocol was that mussels in the earlier study were immersed the entire time (although Schneider (2008) reported a similar result in that mussels immersed continuously grew better than those with a 6-h immersion cycle, despite comparable food rations). Presumably, the daily emersion cycle experienced by mussels in the current study was enough to tip the balance of "scope for growth"—energy available for growth after basic metabolic needs are met (Widdows and Johnson, 1988)—from positive to neutral or negative, either due to decreased feeding time (unlikely as the mussels were generally able to clear the available food each day) or increased stress during aerial exposure unrelated to temperature (*e.g.,* hypoxia and associated hypercapnia [elevated CO_2]; Burnett and Stickle, 2001). For this reason, we did not compare shell growth among treatment groups, but instead used size-specific dry tissue mass (*i.e.,* physiological condition) with a general linear model incorporating final shell length as a covariate. One concern with such an approach is that if shell and soft tissue do not grow simultaneously, a condition index based on tissue mass adjusted to a standard length may not represent true productivity levels (Hilbish, 1986). This should not be a problem in our study, as there was no measureable shell growth in any of the treatments, and our statistical results and conclusions were unchanged when we removed mussel length as a covariate from the model.

Individuals receiving a low food ration or exposed to chronic heat stress during daily emersion had significantly less tissue mass at the end of the experiment than mussels given a high food ration or exposed to low stress. There was also, however, some evidence of an interaction between food and temperature (Table 1; Fig. 3). Although mussels in both food groups exhibited a reduction in tissue mass when exposed to chronic heat stress, the decrease was not statistically significant in the low-food group and was proportionally smaller than the decrease observed in the high-food group (9% *vs.* 15%, respectively). Mean dry tissue mass (adjusted for minor differences in final shell length) of mussels in the high-food, low-stress treatment was significantly greater than that of mussels in any of the other treatment groups and was comparable to that of mussels collected from the field at the beginning of the experiment. In other words, although mussels in this treatment group did not grow, neither did they lose tissue mass. We ignored block as a factor in the final model since there was no evidence of an effect ($F_{11, 32} = 0.85$, $P = 0.595$; Winer *et*

Table 1

General linear model of the effects of food ration and chronic temperature stress on mean dry tissue mass of California mussels after 8 weeks, with final shell length as a covariate

Source	df	MS	F	P
Shell length	1	1.486	6.66	0.013
Food ration	1	2.080	9.33	0.004
Temperature stress	1	1.730	7.76	0.008
Food × temperature	1	0.858	3.85	0.056
Residual	43	0.223	–	–

Data (shell length and tissue mass) were transformed with a $\ln(x + 1)$ function to remove variance heterogeneity and the assumption of homogeneity of slopes tested prior to analysis.

al., 1991). Although observed reductions in size-specific tissue mass in some treatments could in principle indicate spawning rather than negative scope for growth, this is unlikely as the mussels in our experiment were probably not yet of reproductive size (Suchanek, 1981) and we saw no evidence of gonad development or gamete release during the entire period.

Acute heat stress and mussel survival

At the end of the experiment manipulating food ration and chronic heat stress, there were significant differences
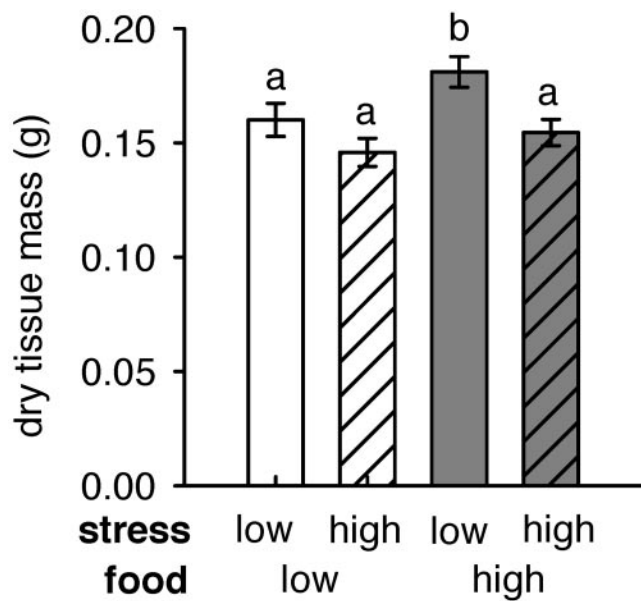

Figure 3. Size-specific dry tissue mass of mussels (mean ± SE; $n = 12$ experimental units (beakers) per treatment group, 3 mussels per beaker) as a function of prior thermal history during daily aerial exposure and food ration (low stress [18–20 °C; *open bars*]; high stress [32 °C; *hatched bars*]; low food [~12 μg chl *a* per mussel per day; *white bars*]; and high food [~148 μg chl *a* per mussel per day; *gray bars*]). Different letters indicate significant differences among treatment groups at the $\alpha = 0.05$ level with Tukey's HSD test following a significant test of main effects in a general linear model with final shell length as a covariate.

among treatment groups with respect to survival following subsequent exposure to more extreme body temperatures (CMH Chi-Square = 11.78, df = 3, $P = 0.008$; Fig. 4). In general, access to greater food resources and prior exposure to heat stress were associated with higher frequencies of survival. Across experimental temperatures, mussels in the high-food, high-stress group survived the best, whereas those in the low-food, low-stress group did the worst. Overall survival decreased with increasing peak body temperature. Our observation that only a few mussels died after exposure to 36 °C, but most died after exposure to 42 °C, matches well with lethal thermal tolerance limits for this species measured on field-collected individuals (Denny *et al.*, 2011).

Discussion

This study provides support for the idea that acclimatory responses to sublethal temperature stress can drive a trade-off between survival and competing life-history traits, as predicted by theory. Intertidal mussels experiencing higher average daily maximum temperatures during aerial exposure in the field grew less than those living in cooler locations on the shore, and individuals exposed to daily heat stress in the laboratory exhibited a decrease in size-specific tissue mass relative to unstressed individuals. At the same time, prior thermal conditioning resulted in higher proportional survival following acute exposure to more extreme temperatures, indicative of successful activation of the heat-shock response. Experimental mussels in the high-food, high-stress group had condition levels comparable to those of mussels in the low-food groups but survived at a much higher rate, consistent with the idea that individuals paying lower marginal costs will allocate more energy to defense when necessary (Cohen and Mangel, 1999). Overall, mussels receiving less food had poor condition and survival relative to individuals fed more, suggesting that individuals with limited access to resources are less able to mitigate potential costs of thermal stress through physiological mechanisms (see also Krebs and Loeschcke, 1994; Schneider *et al.*, 2010). Expected increases in air and water temperatures (Kordas *et al.*, 2011) coupled with potential decreases in phytoplankton productivity (Behrenfeld *et al.*, 2006) over the coming decades could therefore pose a significant physiological challenge to many species.

The responses of intertidal organisms to variation in temperature and food are complex, however. Recent studies have found growth rates of mussels to be positively related to local seawater temperature (Blanchette *et al.*, 2007), food availability (Krenz *et al.*, 2011), or both (Menge *et al.*, 2008); and negatively related to maximum temperature during aerial exposure (Schneider, 2008; this study). Positive effects of higher water temperature on growth likely represent physiological rate effects, changes in the rates of bio-
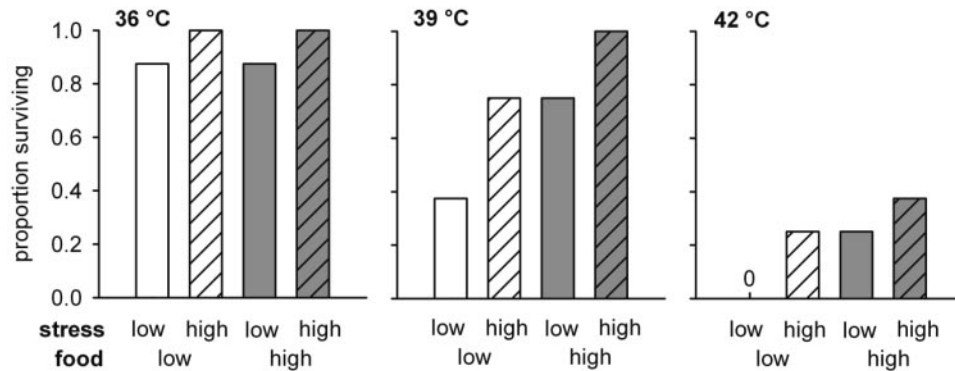
Figure 4. Proportion of mussels surviving for 24 h after an acute exposure to body temperatures of 36, 39, or 42 °C during a simulated low tide ($n = 8$ individuals per group) at the end of the 8-week chronic stress experiment. Mussels varied with respect to prior thermal history and food ration (low stress [open bars]; high stress [hatched bars]; low food [white bars]; and high food [gray bars]). The observed association between treatment group and survival, controlling for temperature, was statistically significant (CMH Chi-Square = 11.78, df = 3, $P = 0.008$).

logical processes due to nonstressful thermal effects at the molecular and cellular levels (Sanford, 2002). In contrast, negative effects of high temperatures during emersion are presumably caused by stress (*e.g.,* Dahlhoff *et al.*, 2002; Pincebourde *et al.*, 2008). Temperature and desiccation stress have also been implicated in observed reductions in reproductive effort by intertidal mussels higher on the shore relative to those at lower elevations (Petes *et al.*, 2007, 2008), although potential effects of differential food availability cannot be discounted. At the same time, individuals living in more stressful locations tend to exhibit higher levels of heat-shock proteins and are more tolerant of temperature extremes (Helmuth and Hofmann, 2001; Somero, 2002; Dong *et al.*, 2008), as expected if trade-offs exist. Such changes in the relative allocation of resources to important demographic rates can have dramatic effects on individual fitness, population growth trajectories, and the direction and intensity of interactions among species (Caswell, 2001; Boyce *et al.*, 2006; Pincebourde *et al.*, 2008).

Along with temperature, food availability is one of the most important environmental predictors of mussel growth (Winter, 1978; Bayne and Newell, 1983; but see Phillips, 2005). Multiple factors interact to determine food availability to mussels, including local primary productivity, water flow rates, population densities, and for intertidal organisms, time spent immersed (Bayne and Newell, 1983; Seed and Suchanek, 1992; Allen and Williams, 2003). Spatial and temporal variation in food quality (*e.g.,* particle size distribution, biochemical composition, and inorganic seston load) also influences mussel energy budgets, with higher growth rates generally associated with higher quality food (Bayne and Worrall, 1980; Navarro and Thompson, 1995). One approach to quantifying the combined effects of environmental temperatures and resource availability on organismal performance is dynamic energy budget (DEB) mod-

eling. DEB models describe the rates at which organisms acquire and use energy for physiological processes (Kooijman, 2010). Researchers have recently begun combining DEB models that use body temperatures and local food availability as input parameters to determine individual fluxes and pools of energy, with biophysical ecological (BE) approaches (*e.g.,* heat budget models; Helmuth, 1998; Denny and Harley, 2006) that produce body temperatures as outputs based on water temperature, solar radiation, air temperature, ground temperature and wind speed (Kearney *et al.*, 2010; Sarà *et al.*, 2011). By parameterizing coupled DEB and BE models from archived weather and chlorophyll *a* data, Sarà *et al.* (2011) were able to successfully predict the presence, absence, and maximum size of intertidal and subtidal individuals of *Mytilus galloprovinciales* at three Mediterranean sites. Oceanographic models explaining variation in phytoplankton quantity and quality could be similarly incorporated. Although many details remain to be worked out, this sort of integrative approach has the potential to substantially improve our understanding of the mechanistic linkages between local environmental conditions and individual physiology and demography.

Not all studies on rocky shores have found negative correlations between different life-history traits in response to stress. In an experimental manipulation of food and heat stress to intertidal whelks, Dahlhoff *et al.* (2002) showed that snails in warm wave-protected areas with access to prey had both higher metabolic rates and levels of Hsp70 expression compared to individuals without access to food, contrary to predictions of a trade-off. Similarly, seaweeds exposed to similar temperature and desiccation stress but with more time for daily photosynthesis exhibited the same or higher survival, growth, reproduction, and anti-herbivore chemical defenses as individuals with less time to gain energy (Dethier *et al.*, 2005). Intertidal blue mussels (*Myti-*
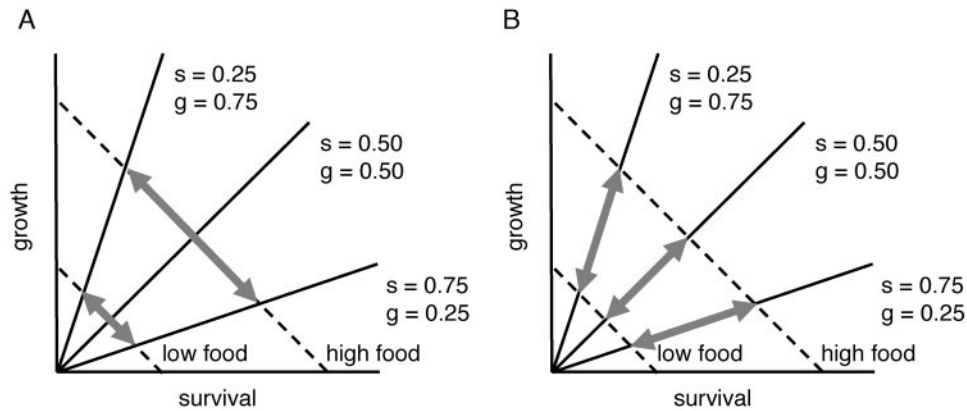
Figure 5. Conceptual model of the relationship between local resource availability and observed patterns of resource allocation; after van Noordwijk and de Jong (1986). Solid lines represent different levels of allocation between two competing life-history traits (*e.g.,* survival and growth) whereas dashed lines represent different levels of resource availability. At a given level of resource availability, an increase in allocation to one trait necessarily results in a decrease in allocation to the other, resulting in a negative relationship (gray arrows, Fig. 5a). In contrast, if the level of available resources varies such that some individuals have access to more than others, they can allocate more resources to both traits, resulting in a positive relationship (gray arrows, Fig. 5b).

lus edulis) at sites characterized by high temperature and food availability expressed more inducible stress proteins compared to mussels at cooler sites with less food, but they were also in better condition and exhibited higher growth potential (Lesser *et al.*, 2010). These (and our) observations suggest a conceptual model of the relationship between local resource availability and patterns of allocation among individuals (Fig. 5; after van Noordwijk and de Jong, 1986). Given a finite amount of resources, increasing allocation to one physiological process decreases the amount available for others, leading to negative correlations between levels of trait expression (Fig. 5a; Stearns, 1992). However, such trade-offs need not occur across resource levels, as individuals with more resources at their disposal can allocate greater amounts to all aspects of their life history (Fig. 5b; Tuomi *et al.*, 1983). An important implication of this idea is that forecasting the effects of climate change in rocky intertidal ecosystems will require understanding not just how organisms respond to different temperature regimes, but also how variation in local resource availability modifies those responses.

Ignoring variation in food resources, the impact of temperature stress on individuals is a function of the frequency, intensity, and duration of imposed environmental extremes (Benedetti-Cecchi, 2003; Boyce *et al.*, 2006; Denny *et al.*, 2009). Little is currently known, however, about the relative importance of these factors or their interaction, and existing data suggest that disentangling these effects will be difficult. Although we found a positive effect of prior sublethal stress on survival following a subsequent acute exposure, other researchers have reported that repeated high-stress events can lead to a rapid decline in temperature tolerance as measured by LT_{50}, the temperature lethal to 50% of the individuals in a population (Jones *et al.*, 2009; Sorte *et al.*, 2011). Pincebourde *et al.* (2008) found that acute exposure to high (but sublethal) aerial body temperatures had positive effects on feeding rates and no effect on growth of the intertidal sea star *Pisaster ochraceus*, but that chronic exposure had negative effects on both. Effects of chronic exposure to high aerial temperatures on growth and survival may also vary depending upon the water temperature to which organisms are acclimated (Schneider, 2008). To complicate matters further, observed differences in thermal physiology among geographically separate populations may be due to genetic variation (local adaptation), developmental canalization, or maternal effects, rather than to phenotypic plasticity (Kuo and Sanford, 2009; Logan *et al.*, 2012).

Nevertheless, understanding how key species respond to environmental variation at the individual level is critical if we are to successfully anticipate the effects of future perturbations on the persistence of local populations, species' geographic distributions, and the outcomes of species' interactions that determine community structure and function (*e.g.,* Helmuth *et al.*, 2006; Denny *et al.*, 2009; Kordas *et al.*, 2011). For example, it is likely that reduced growth of mussels in response to low food availability or high stress will affect multiple levels of biological organization. Lower fecundity is an inevitable consequence of smaller body size for many invertebrates, with potential negative consequences for dispersal, recruitment, and long-term population persistence (Seed and Suchanek, 1992; Ólafsson *et al.*, 1994). Rapid growth is also an important factor in determining the competitive dominance of mussels on rocky shores, allowing them to overgrow other organisms and offset mortality from predators or disturbance to maintain spatial percent cover (Petraitis, 1995). Changes in compet-

itive hierarchies within rocky intertidal communities can lead to rapid and large-scale reorganization, with dramatic effects on ecosystem processes that include primary productivity, energy and nutrient cycling, and habitat provisioning (Paine, 1966; Seed and Suchanek, 1992; Wootton, 1994). Subsequent investigations should focus on quantifying the effects of temperature stress and food availability on the actual heat-shock response (*e.g.,* with new approaches such as proteomics; Tomanek and Zuzow, 2010), examining the role of variation in thermal history on organismal performance, and documenting the degree to which these factors alter physiological and behavioral outcomes in the field.

Acknowledgments

Literature Cited

Allen, B. J., and S. L. Williams. 2003. Native eelgrass *Zostera marina* controls growth and reproduction of an invasive mussel through food limitation. *Mar. Ecol. Prog. Ser.* **254:** 57–67.

Allen, S. M., and L. E. Burnett. 2008. The effects of intertidal air exposure on the respiratory physiology and the killing activity of hemocytes in the pacific oyster, *Crassostrea gigas* (Thunberg). *J. Exp. Mar. Biol. Ecol.* **357:** 165–171.

Bayne, B. L., and R. C. Newell. 1983. Physiological energetics of marine molluscs. Pp. 407–515 in *The Mollusca: Physiology,* Part 1, Vol. 4, A. S. M. Saleuddin and K. M. Wilbur, eds. Academic Press, New York.

Bayne, B. L., and C. M. Worrall. 1980. Growth and production of mussels *Mytilus edulis* from two populations. *Mar. Ecol. Prog. Ser.* **3:** 317–328.

Bayne, B. L., C. J. Bayne, T. C. Carefoot, and R. J. Thompson. 1976. The physiological ecology of *Mytilus californianus* Conrad. 2. Adaptations to low oxygen tension and air exposure. *Oecologia* **22:** 229–250.

Behrenfeld, M. J., K. Worthington, R. M. Sherrell, F. P. Chavez, P. Strutton, M. McPhaden, and D. M. Shea. 2006. Controls on tropical Pacific Ocean productivity revealed through nutrient stress. *Nature* **442:** 1025–1028.

Benedetti-Cecchi, L. 2003. The importance of the variance around the mean effect size of ecological processes. *Ecology* **84:** 2335–2346.

Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lesson from intertidal habitats. *Ecology* **78:** 1976–1989.

Blanchette, C. A., B. Helmuth, and S. D. Gaines. 2007. Spatial patterns of growth in the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. *J. Exp. Mar. Biol. Ecol.* **340:** 126–148.

Boyce, M. S., C. V. Haridas, and C. T. Lee. 2006. Demography in an increasingly variable world. *Trends Ecol. Evol.* **21:** 141–148.

Buckley, B. A., M. Owen, and G. E. Hofmann. 2001. Adjusting the thermostat: the threshold induction temperature for the heat-shock response in intertidal mussels (genus *Mytilus*) changes as a function of thermal history. *J. Exp. Biol.* **204:** 3571–3579.

Burnett, L. E., and W. B. Stickle. 2001. Physiological responses to hypoxia. Pp. 101–114 in *Coastal Hypoxia: Consequences for Living Resources and Ecosystems,* N. N. Rabalais and R. E. Turner, eds. American Geophysical Union, Washington, D.C.

Caswell, H. 2001. *Matrix Population Models.* Sinauer Associates, Sunderland, MA.

Cohen, D., and M. Mangel. 1999. Investing for survival of rare severe stresses in heterogeneous environments. *Evol. Ecol. Res.* **1:** 987–1002.

Connell, J. H. 1961. Influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42:** 710–723.

Dahlhoff, E. P., and B. A. Menge. 1996. Influence of phytoplankton concentration and wave exposure on the ecophysiology of *Mytilus californianus*. *Mar. Ecol. Prog. Ser.* **144:** 97–107.

Dahlhoff, E. P., B. A. Buckley, and B. A. Menge. 2001. Physiology of the rocky intertidal predator *Nucella ostrina* along an environmental stress gradient. *Ecology* **82:** 2816–2829.

Dahlhoff, E. P., J. H. Stillman, and B. A. Menge. 2002. Physiological community ecology: variation in metabolic activity of ecologically important rocky intertidal invertebrates along environmental gradients. *Integr. Comp. Biol.* **42:** 862–871.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* **41:** 351–389.

Denny, M. W., and C. D. G. Harley. 2006. Hot limpets: predicting body temperature in a conductance-mediated thermal system. *J. Exp. Biol.* **209:** 2409–2419.

Denny, M. W., B. Helmuth, G. H. Leonard, C. D. G. Harley, L. J. H. Hunt, and E. K. Nelson. 2004. Quantifying scale in ecology: lessons from a wave-swept shore. *Ecol. Monogr.* **74:** 513–532.

Denny, M. W., L. P. Miller, and C. D. G. Harley. 2006. Thermal stress on intertidal limpets: long-term hindcasts and lethal limits. *J. Exp. Biol.* **209:** 2420–2431.

Denny, M. W., L. J. H. Hunt, L. P. Miller, and C. D. G. Harley. 2009. On the prediction of extreme ecological events. *Ecol. Monogr.* **79:** 397–421.

Denny, M. W., W. W. Dowd, L. Bilir, and K. J. Mach. 2011. Spreading the risk: small-scale body temperature variation among intertidal organisms and its implications for species persistence. *J. Exp. Mar. Biol. Ecol.* **400:** 175–190.

Dethier, M. N., S. L. Williams, and A. Freeman. 2005. Seaweeds under stress: manipulated stress and herbivory affect critical life-history functions. *Ecol. Monogr.* **75:** 403–418.

Dong, Y., L. P. Miller, J. G. Sanders, and G. N. Somero. 2008. Heat-shock protein 70 (Hsp70) expression in four limpets of the genus *Lottia*: Interspecific variation in constitutive and inducible synthesis correlates with *in situ* exposure to heat stress. *Biol. Bull.* **215:** 173–181.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Atmospheric science: climate extremes: observations, modeling, and impacts. *Science* **289:** 2068–2074.

Fitzhenry, T., P. M. Halpin, and B. Helmuth. 2004. Testing the effects

of wave exposure, site, and behavior on intertidal mussel body temperatures: applications and limits of temperature logger design. *Mar. Biol.* **145:** 339–349.

Gaines, S. D., and M. W. Denny. 1993. The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. *Ecology* **74:** 1677–1692.

Gedan, K. B., J. Bernhardt, M. D. Bertness, and H. M. Leslie. 2011. Substrate size mediates thermal stress in the rocky intertidal. *Ecology* **92:** 576–582. .

Halpin, P. M., B. A. Menge, and G. E. Hofmann. 2004. Experimental demonstration of plasticity in the heat shock response of the intertidal mussel *Mytilus californianus*. *Mar. Ecol. Prog. Ser.* **276:** 137–145.

Harley, C. D. G. 2008. Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. *Mar. Ecol. Prog. Ser.* **371:** 37–46.

Helmuth, B., C. D. G. Harley, P. M. Halpin, M. O'Donnell, G. E. Hofmann, and C. A. Blanchette. 2002. Climate change and latitudinal patterns of intertidal thermal stress. *Science* **298:** 1015–1017.

Helmuth, B., N. Mieszkowska, P. Moore, and S. J. Hawkins. 2006. Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. *Annu. Rev. Ecol. Evol. Syst.* **37:** 373–404.

Helmuth, B. S. T. 1998. Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate. *Ecol. Monogr.* **68:** 51–74.

Helmuth, B. S. T., and G. E. Hofmann. 2001. Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. *Biol. Bull.* **201:** 374–384.

Hilbish, T. J. 1986. Growth trajectories of shell and soft tissue in bivalves: seasonal variation in *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.* **96:** 103–113.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54:** 187–211.

Jones, S. J., N. Mieszkowska, and D. S. Wethey. 2009. Linking thermal tolerances and biogeography: *Mytilus edulis* (L.) at its southern limit on the east coast of the United States. *Biol. Bull.* **217:** 73–85.

Jost, J., and B. Helmuth. 2007. Morphological and ecological determinants of body temperature of *Geukensia demissa*, the Atlantic ribbed mussel, and their effects on mussel mortality. *Biol. Bull.* **213:** 141–151.

Kearney, M., S. J. Simpson, D. Raubenheimer, and B. Helmuth. 2010. Modelling the ecological niche from functional traits. *Philos. Trans. R. Soc. B* **365:** 3469–3483.

Kooijman, S. A. L. M. 2010. *Dynamic Energy Budget Theory for Metabolic Organization*. Cambridge University Press, Cambridge.

Kordas, R. L., C. D. G. Harley, and M. I. O'Connor. 2011. Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. *J. Exp. Mar. Biol. Ecol.* **400:** 218–226.

Krebs, R. A., and V. Loeschcke. 1994. Costs and benefits of activation of the heat-shock response in *Drosophila melanogaster*. *Funct. Ecol.* **8:** 730–737.

Krenz, C., B. A. Menge, T. L. Freidenburg, J. Lubchenco, F. Chan, M. M. Foley, and K. J. Nielsen. 2011. Ecological subsidies to rocky intertidal communities: linear or non-linear changes along a consistent geographic upwelling transition? *J. Exp. Mar. Biol. Ecol.* **409:** 361–370.

Kültz, D. 2003. Evolution of the cellular stress proteome: from monophyletic origin to ubiquitous function. *J. Exp. Biol.* **206:** 3119–3124.

Kuo, E. S. L., and E. Sanford. 2009. Geographic variation in the upper thermal limits of an intertidal snail: implications for climate envelope models. *Mar. Ecol. Prog. Ser.* **388:** 137–146.

Lesser, M. P., M. A. Bailey, D. G. Merselis, and J. R. Morrison. 2010. Physiological response of the blue mussel *Mytilus edulis* to differences in food and temperature in the Gulf of Maine. *Comp. Biochem. Physiol. A* **156:** 541–551.

Logan, C. A., L. E. Kost, and G. N. Somero. 2012. Latitudinal differences in *Mytilus californianus* thermal physiology. *Mar. Ecol. Prog. Ser.* **450:** 93–105.

Lucas, A. J., P. J. S. Franks, and C. L. Dupont. 2011. Horizontal internal-tide fluxes support elevated phytoplankton productivity over the inner continental shelf. *Limnol. Oceanogr. Fluids Environ.* **1:** 56–74.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.* **46:** 355–393.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* **130:** 730–757.

Menge, B. A., F. Chan, and J. Lubchenco. 2008. Response of a rocky intertidal ecosystem engineer and community dominant to climate change. *Ecol. Lett.* **11:** 151–162.

Navarro, J. M., and R. J. Thompson. 1995. Seasonal fluctuations in the size-spectra, biochemical composition and nutritive value of the seston available to a suspension-feeding bivalve in a subarctic environment. *Mar. Ecol. Prog. Ser.* **125:** 95–106.

Ólafsson E. B., C. H. Peterson, and W. G. Ambrose, Jr. 1994. Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanogr. Mar. Biol. Annu. Rev.* **32:** 65–109.

Paine, R. T. 1966. Food web complexity and species diversity. *Am. Nat.* **100:** 65–75.

Petes, L. E., B. A. Menge, and G. D. Murphy. 2007. Environmental stress decreases survival, growth, and reproduction in New Zealand mussels. *J. Exp. Mar. Biol. Ecol.* **351:** 83–91.

Petes, L. E., B. A. Menge, and A. L. Harris. 2008. Intertidal mussels exhibit energetic trade-offs between reproduction and stress resistance. *Ecol. Monogr.* **78:** 387–402.

Petraitis, P. S. 1995. The role of growth in maintaining spatial dominance by mussels (*Mytilus edulis*). *Ecology* **76:** 1337–1346.

Phillips, N. E. 2005. Growth of filter-feeding benthic invertebrates from a region with variable upwelling intensity. *Mar. Ecol. Prog. Ser.* **295:** 79–89.

Pincebourde, S., E. Sanford, and B. Helmuth. 2008. Body temperature during low tide alters the feeding performance of a top intertidal predator. *Limnol. Oceanogr.* **53:** 1562–1573.

Roberts, D. A., G. E. Hofmann, and G. N. Somero. 1997. Heat-shock protein expression in *Mytilus californianus*: acclimatization (seasonal and tidal-height comparisons) and acclimation effects. *Biol. Bull.* **192:** 309–320.

Sanford, E. 2002. Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. *Integr. Comp. Biol.* **42:** 881–891.

Sarà, G., M. Kearney, and B. Helmuth. 2011. Combining heat-transfer and energy budget models to predict thermal stress in Mediterranean intertidal mussels. *Chem. Ecol.* **27:** 135–145.

Schneider, K. R. 2008. Heat stress in the intertidal: comparing survival and growth of an invasive and native mussel under a variety of thermal conditions. *Biol. Bull.* **215:** 253–264.

Schneider, K. R., L. E. Van Thiel, and B. Helmuth. 2010. Interactive effects of food availability and aerial body temperature on the survival of two intertidal *Mytilus* species. *J. Therm. Biol.* **35:** 161–166.

Seed, R., and T. H. Suchanek. 1992. Population and community ecology of *Mytilus*. Pp. 87–169 in *The Mussel* Mytilus*: Ecology, Physiology, Genetics and Culture*, E. Gosling, ed. Elsevier Science, Amsterdam.

Somero, G. N. 2002. Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integr. Comp. Biol.* **42:** 780–789.

Sorte, C. J. B., S. J. Jones, and L. P. Miller. 2011.   Geographic variation in temperature tolerance as an indicator of potential population responses to climate change. *J. Exp. Mar. Biol. Ecol.* **400:** 209–217.

Stearns, S. C. 1992.   *The Evolution of Life Histories.* Oxford University Press, Oxford.

Stillman, J. H. 2003.   Acclimation capacity underlies susceptibility to climate change. *Science* **301:** 65.

Suchanek, T. H. 1981.   The role of disturbance in the evolution of life history strategies in the intertidal mussels *Mytilus edulis* and *Mytilus californianus. Oecologia* **50:** 143–152.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. Ferreira de Siqueira, A. Grainger, L. Hannah *et al.* 2004.   Extinction risk from climate change. *Nature* **427:** 145–148.

Tomanek, L., and M. J. Zuzow. 2010.   The proteomic response of mussel congeners *Mytilus galloprovincialis* and *M. trossulus* to acute heat stress: implications for thermal tolerance limits and metabolic costs of thermal stress. *J. Exp. Biol.* **213:** 3559–3574.

Tuomi, J., T. Hakala, and E. Haukioja. 1983.   Alternative concepts of reproductive effort, costs of reproduction, and selection in life-history evolution. *Am. Zool.* **23:** 25–34.

van Noordwijk, A. J., and G. de Jong. 1986.   Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* **128:** 137–142.

Widdows, J., and D. Johnson. 1988.   Physiological energetics of *Mytilus edulis*: scope for growth. *Mar. Ecol. Prog. Ser.* **46:** 113–121.

Winer, B. J., D. R. Brown, and K. M. Michels. 1991.   *Statistical Principles in Experimental Design.* McGraw-Hill, New York.

Winter, J. E. 1978.   A review on the knowledge of suspension-feeding in Lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture* **13:** 1–33.

Wootton, J. T. 1994.   Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* **75:** 151–165.