Reports

Ecology, 96(4), 2015, pp. 902–907

A biophysical basis for patchy mortality during heat waves

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Abstract. Extreme heat events cause patchy mortality in many habitats. We examine biophysical mechanisms responsible for patchy mortality in beds of the competitively dominant ecosystem engineer, the marine mussel *Mytilus californianus*, on the west coast of the United States. We used a biophysical model to predict daily fluctuations in body temperature at sites from southern California to Washington and used results of laboratory experiments on thermal tolerance to determine mortality rates from body temperature. In our model, we varied the rate of thermal conduction within mussel beds and found that this factor can account for large differences in body temperature and consequent mortality during heat waves. Mussel beds provide structural habitat for other species and increase local biodiversity, but, as sessile organisms, they are particularly vulnerable to extreme weather conditions. Identifying critical biophysical mechanisms related to mortality and ecological performance will improve our ability to predict the effects of climate change on these vulnerable ecosystems.

Key words: climate; extreme events; heat transfer; intertidal zone; mussel; Mytilus californianus; *thermal conductivity; thermal stress.*

INTRODUCTION

Extreme heat events have increased in frequency and duration over recent decades (e.g., Della-Marta et al. 2007, Perkins and Alexander 2013, Oswald and Rood 2014) and are expected to increase in frequency and severity under future climate scenarios (Meehl and Tebaldi 2004, Fischer and Schär 2010). In addition, there is an upward trend in the temperatures of the hottest days and nights (Christidis et al. 2005). The consequences of heat waves can be severe as evidenced by die-offs following heat waves in both terrestrial and marine ecosystems (e.g., desert birds, McKechnie and Wolf 2010; forests, Allen et al. 2010; coral reefs, Hughes et al. 2003; mussel beds, Tsuchiya 1983, Harley 2008). In many cases, however, mortality is spatially patchy, making it difficult to quantify the statistical significance of the impact of the heat wave event (Hughes et al. 2003, Harley 2008, Allen et al. 2010).

Heat waves are especially stressful for plants and sessile animals, which are unable to move to thermal refuges. Plants and sessile animals are also ectotherms and therefore are unable to regulate their body temperature using metabolic energy. Instead, ectotherm body temperatures are determined by meteorological conditions, including solar radiation, temperature, humidity, and wind speed, and organismal traits including size, color, and shape. Most sessile ectotherms tolerate a wide range of body temperatures, but, during heat waves, body temperatures are likely to exceed tolerance ranges. One of the keys to predicting the spatial distribution of lethality is to determine body temperatures over a broad range of spatial and temporal scales. Predictions of organismal body temperatures can be obtained with biophysical models, which use meteorological data to calculate the exchanges of heat between an organism and the environment (e.g., Gates 2003). High-resolution weather data for forcing biophysical body temperature models are increasingly available (Mislan and Wethey 2011), providing an opportunity to identify mechanisms responsible for spatial variability in mortality during extreme events.

We use rocky intertidal shores to examine the causes of patchy mortality because intertidal shores have sharp environmental gradients and complex topography over spatial scales of a few meters. The environmental gradients in the intertidal are largely related to tidal immersion of the substratum, usually twice per day. During high tides, the intertidal zone is covered by the ocean, and during low

Manuscript received 24 June 2014; revised 10 November 2014; accepted 21 November 2014. Corresponding Editor: S. G. Morgan.

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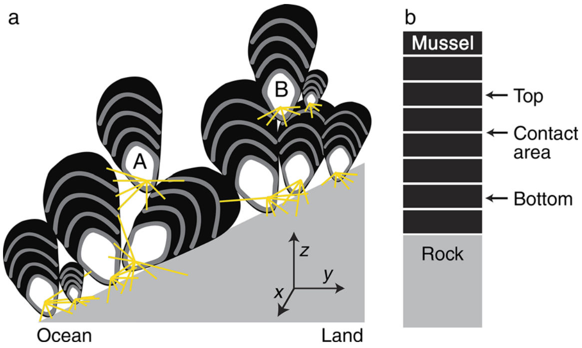

FIG. 1. (a) Cross-section of the structure of a multilayer mussel bed in the y-, z-plane. The mussels conduct heat to other mussels through direct contact that varies among individuals. Mussel A is suspended by byssal threads and has a low percentage contact area with underlying mussels. Mussel B has a high percentage contact area with underlying mussels. (b) A diagram of the one-dimensional biophysical model. The mussel bed is divided into eight layers (black boxes) that are 1 cm thick and then connected to the rock (gray box). Contact area varies the amount of conductive heat transfer between the fourth and fifth layers of the mussel bed; 10% contact means that 10% of the heat from the fourth layer is transferred to the fifth layer.

tides, it is exposed to aerial conditions. Intertidal organisms are most vulnerable to heat wave events when low tides occur during midday and the weather is sunny (Helmuth et al. 2002, 2006, Denny et al. 2009). Organisms living at the highest shore levels are exposed to aerial conditions for the longest time periods and are most likely to be exposed to the highest temperatures. Therefore, greater mortality from heat waves would be expected at higher shore levels (e.g., Wethey 1984).

We chose intertidal mussels as our model organisms to study patchiness in thermal death because they are ecologically dominant and can occupy broad swaths of space (e.g., Paine 1974). Mussels tend to group together and create a complex matrix of mussels and byssal attachment threads called beds that are up to several mussels deep. This complex bed structure traps water and sediment, and its interstices form a cool, wet microhabitat for juvenile and adult mussels and many other species (Suchanek 1978). Because of the steep gradients in temperature and humidity in mussel beds, we expect that bed structure would have a strong influence on patchiness of mortality. Mortality has been observed in mussel beds after periods of exceptionally high temperatures. For example, Tsuchiya (1983) observed complete elimination of a mussel bed after a heat wave. More often, dead mussels are patchily distributed throughout the mussel beds (Suchanek 1978, Petes et al. 2007, Harley 2008). Mussel mortality rates were predicted to be highest at the highest shore levels (e.g., Mislan et al. 2014), but Harley (2008) found mortality at lower shore levels. Harley (2008) also found that mortality occurred almost exclusively on the surface of the bed, where there was a range of mussel mortality rates even for the angles of solar incidence with relatively more dead mussels. Because of the multilayer structure of mussel beds, we suspect that heat conduction to underlying substrates, mussels, and rock is an important moderating influence on body temperatures and survival during heat wave events. Mussels directly exposed to solar radiation on the surface of the bed and with low contact with the substrate below would be expected to be the hottest and die at the highest rates (Fig. 1). The contact area between mussels is highly variable, and mussels with low contact with underlying substrates are likely distributed throughout the mussel bed. Therefore, the distribution of dead mussels following heat waves would be predicted to be patchy and would not necessarily be restricted to the highest shore levels. In this study, we use a biophysical model to determine the sensitivity of body temperatures and thermal mortality to the contact area within mussel beds along a latitudinal gradient on the west coast of North America.

METHODS

The biophysical model of mussel body temperature was developed from a meteorological land surface model modified to mimic the thermal properties of a mussel bed exposed to tidal inundation and wave run-up (described in detail in Wethey et al. 2011). The model has mussel layers with the heat transfer characteristics of *M. californianus* mussels, which have black shells and internal tissue composed mostly of water (Fig. 1b). The total mussel bed depth is 8 cm and is simulated in the model as 8 × 1-cm mussel layers. The mussel layers are on top of impermeable rock. Other organisms that live in mussel beds are not currently included in the model. Mussel temperatures and survival were calculated for 3 cm depth (top) and 7 cm depth (bottom) to analyze the effect of position within a multilayer bed (Fig. 1b). Depths of 3 cm and 7 cm were selected to represent the core temperatures of 4-cm mussels on the top and bottom of a multilayer mussel bed because 4-cm mussels are the median size of adult *Mytilus californianus* on exposed shores (Suchanek 1981).

TABLE 1. Coordinates and shore levels of contiguous upper zonation limits for *Mytilus californianus* mussel beds along the west coast of North America (Mislan et al. 2014).

Site	Latitude (°N)	Longitude (°W)	Shore level above MLLW (m)
Tatoosh Island	48.39	124.74	2.39
Boiler Bay	44.83	124.06	1.88
Strawberry Hill	44.25	124.11	2.02
Cape Arago	43.31	124.40	1.82
Trinidad	41.06	124.15	2.02
Cape Mendocino	40.35	124.36	1.77
Bodega Bay	38.32	123.07	1.86
Santa Cruz	36.95	122.06	1.69
Pacific Grove	36.62	121.90	1.74
Cambria	35.54	121.09	1.45
Jalama	34.50	120.50	1.44
Alegria	34.47	120.28	1.25
SCI Fraser	34.06	119.92	1.09
SCI Prisoners	34.02	119.69	1.34
SCI Willows	33.96	119.76	1.36

Note: SCI is Santa Cruz Island in Channel Islands National Park, USA; MLLW is mean lower low water.

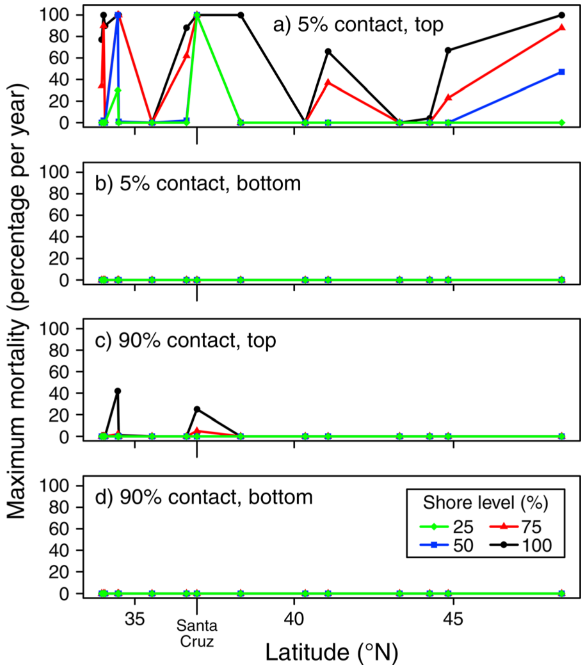

FIG. 2. Latitudinal variation in the maximum mortality in model hindcasts 1997–2007 for the mussel *Mytilus californianus*, showing the effect of contact area within the mussel bed on mortality, at two levels: 5% contact area at the (a) top of the bed and (b) bottom of the bed. The effect of 90% contact area within the mussel bed on mortality at the (c) top of the bed and (d) bottom of the bed. Shore level is the height above mean lower low water (MLLW) of the tides. The shore levels of the contiguous upper limits of the mussel beds were measured at all the sites (Table 1). The percentage refers to the shore level relative to the contiguous upper limit of the mussel bed. For example, if the shore level of the contiguous upper limit of the mussel bed for a given site is 2.0 m above MLLW in Table 1, then the 75% shore level of said site is at 1.5 m (0.75 × 2.0 m). Mussel beds at the lower shore levels (25%) are covered by high tide for longer periods of time than mussel beds at the contiguous upper limit (100%). Survival is higher at the 25% shore level because mussels at the 25% shore level are exposed to terrestrial conditions, especially solar radiation, during low tide that cause high body temperatures for shorter periods of time. Top mussels with 5% contact, and consequently lower heat transfer to the bottom mussels, had higher predicted mortality. At many sites with 5% contact within the bed, predicted mortality occurred within the mussel zone.

Tides with wave run-up inundate the mussel bed at regular intervals at which point the mussel temperatures are equivalent to sea surface temperature. The duration of tidal inundation is determined by shore level. Shore levels of *M. californianus* contiguous bed upper zonation limits were determined relative to mean lower low water (MLLW; the average of the lowest daily water levels over a 19-year tidal epoch) at 15 sites, spanning 14° of latitude along the west coast of the United States (Table 1; Mislan et al. 2014). Mussel body temperatures were modeled at four different shore levels, which were 25%, 50%, 75%, and 100% of the shore level of *M. californianus* contiguous-bed upper zonation limits at each of these sites. Percentages rather than fixed shore levels were used because the upper zonation limits of mussel beds varied by site (Table 1). To determine the effect of heat conduction within the mussel bed on mussel body temperatures and survival, percentage contact between the fourth and fifth mussel layers (Fig. 1b), the middle of the mussel bed, was varied between 0.05–0.90 (i.e., 5–90%) at all four shore levels at all 15 sites. This model configuration is simulating the range of scenarios in which some mussels are suspended by byssal threads and have little contact, 5%, with the underlying mussels (e.g., mussel A in Fig. 1a) and other mussels have solid contact, 90%, with underlying mussels (e.g., mussel B in Fig. 1a).

The mussel body temperature model was forced with gridded meteorological reanalysis data, which were linearly interpolated to the locations of individual sites using the four closest grid points, for the years 1997–2007 (Mislan and Wethey 2011). Meteorological variables were from North American Regional Reanalysis (NARR; Mesinger et al. 2006) and global horizontal solar radiation was from the GCIP (Global Energy and Water Cycle Exchanges Project [GEWEX] Continental Scale International Project) surface radiation budget archive at the University of Maryland (Pinker and Laszlo 1992). Tidal inundation was predicted using the west coast regional model of the Oregon State University Tidal Prediction Software (Egbert and Erofeeva 2002). Sea surface temperatures were obtained from the Naval Research Laboratory Modular Ocean Data Assimilation (Barron and Kara 2006). Wave run-up was calculated from NOAA Wavewatch III CFSRR (Climate Forecast System Reanalysis and Reforecast) high resolution (1/6°) hindcasts (Chawla et al. 2013), using equations from the United States Army Corps of Engineers Coastal Engineering Manual (U.S. Army Corps of Engineers 2002). To calculate predicted survival from the mussel body temperature hindcasts, we used a probit model based on laboratory measurements of mortality as a function of temperature and exposure duration (for details, see Mislan et al. 2014). Accounting for duration using the probit model is important because mussels exposed to high temperature for a short period of time can have a higher survival rate than mussels exposed to a slightly lower temperature for a long period of time. The probit model took the form: $\text{probit}\,(s) = A\log_{10}(\tau) + [Ct + D] - [A\log_{10}(30)]$ where s is survival, t is temperature, τ is duration of exposure, and A, C, and D are determined from regressions of the laboratory measurements. For one day of exposure, A is –3.14, C is –0.93, and D is 42.16. For two successive days of exposure, A is –3.01, C is –0.97, and D is 43.02. For three successive days of exposure, A is –4.09, C is –1.00, and D is 43.64.

RESULTS

Top layer *M. californianus* mussels with 90% contact within the bed had much lower predicted mortality than top layer mussels with 5% contact within the bed at many of the sites examined (Fig. 2a, c). For top layer mussels with 5% contact, maximum predicted mortality was

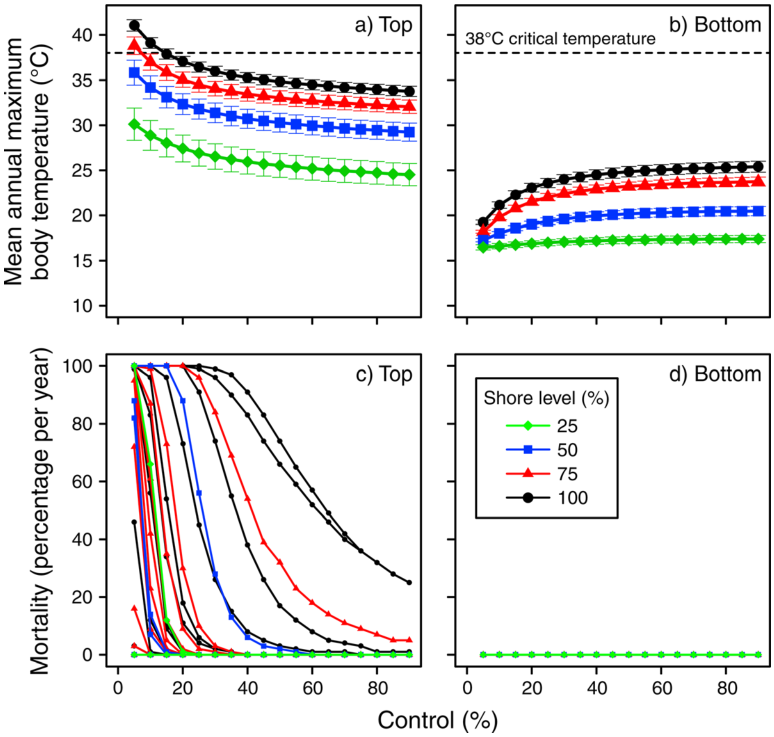

FIG. 3. Effects of within-bed contact (and consequent differences in thermal conductivity) in Santa Cruz, California, USA, on predicted mussel body temperature at the (a) top and (b) bottom and mortality at the (c) top and (d) bottom of mussel beds in model hindcasts 1997–2007. In (a, b), the error bars are standard errors. In (c, d), each line represents one hindcast year. Greater contact within the mussel bed reduced predicted mortality from high temperatures in the top-layer of the mussel bed. For top layer mussels with <20% contact in the bed, predicted mortality due to high temperatures occurred at all shore levels during at least one year.

greater than zero at 12 of the 15 sites at the mussel bed upper shore limits (Fig. 2a). The sites with predicted mortality were distributed throughout the geographic range studied, which encompassed more than 10 degrees of latitude. For top-layer mussels with 90% contact, maximum predicted mortality was only greater than zero at two of the 15 sites at the mussel bed upper shore limits (Fig. 2c). Top-layer mussels with 5% contact had less frequent predicted mortality at low shore levels than at high shore levels (mortality was predicted at 10 sites at the upper quartile of shore levels, at five sites at midshore levels, and at two sites at the lower quartile of shore levels). There was no mortality predicted below the upper quartile of shore levels for top layer mussels with 90% contact. Bottom-layer mussels were not predicted to die from high temperatures during the hindcast period (Fig. 2b, d).

Santa Cruz was the site with the highest predicted mortality at all shore levels in mussel beds with 5% contact (Fig. 2a). Therefore, we examined the effect of contact area on mussel body temperatures and predicted mortality in greater detail at Santa Cruz. Mean annual maximum temperatures and annual maximum mortalities from the model hindcasts were used to evaluate the most extreme environmental conditions experienced by mussels. Top-layer mussels with lower percentage contact area conducted less heat to the underlying substrates and, as a result, had higher predicted body temperatures and mortality on the most thermally stressful days of the year (Fig. 3a, c). The top-layer mussels with 5% contact at higher shore levels (75% and 100% of the upper shore limit of the contiguous *Mytilus californianus* bed) had predicted mean annual maximum temperatures ≥38°C (Fig. 3a). Mean annual maximum predicted temperatures of top layer mussels decreased by at least 4°C as contact within the bed was varied between 5% and 90% (Fig. 3a).

Predicted mortality of top layer mussels was strongly affected by change in contact within the bed (Fig. 3c). Mortality rates of top layer mussels with 5% contact were predicted to be 100% per year at all shore levels during at least one year (Fig. 3c). These mortality rates decreased rapidly to zero as within bed contact increased in all but a few years when mortality remained greater than zero at 90% contact at the highest shore levels (Fig. 3c). The mean annual maximum temperatures of bottom layer mussels were <25°C, and there was no predicted mortality (Fig. 3b, d). The temperatures of bottom layer mussels with 5% contact were lower than those with 90% contact, which is the reverse of the pattern of the top mussels (Fig. 3b).

DISCUSSION

Patchy mortality of mussels after a heat wave was not explained by differences in wave splash or wind speed and was found for mussels at different shore levels with the same substratum orientation (Harley 2008). Our findings indicate that conductive heat transfer could cause patchy mortality patterns in intertidal mussel beds during a heat wave, assuming that there is variability in the percentage contact that individual mussels in the top layers have with the bottom layers of complex mussel beds (Fig. 3). Conductive heat transfer within mussel beds is not the only environmental variable that influences mortality during heat waves. For example, poleward-facing surfaces are cooler than those facing equatorward (e.g., Wethey 1983, Helmuth and Hofmann 2001, Harley 2008), and local variations in wind speed and wave splash may influence temperatures within sites (Denny et al. 2011, Helmuth et al. 2011). However, conductive heat transfer would explain patchy mortality at the scales where live and dead mussels are found within a few centimeters of each other after a heat wave event when all other variables appear to be equal (Petes et al. 2007, Harley 2008). Alternatively, biological variability may be influencing the patchiness in mussel mortality after heat wave events. Potential sources of biological variability include differences in acclimation, adaptation, reproductive state, or parasite load. Heat waves are predicted to increase with climate change, so it is imperative that we understand the physical and biological factors influencing patterns of heat wave related mortality even at very local scales.

Mussels in the top layer of the bed are predicted to die from high temperatures at higher rates than those in the bottom layer of the bed (Fig. 2). We hypothesize that frequent winnowing of top layer mussels with low percentage contact following heat waves leads to thinner mussel beds at sites where mortality due to high temperatures occurs regularly. Smith (2005) surveyed the thickness of mussel beds along the California coast at locations close to those modeled in this study allowing us to make comparisons. Smith (2005) measured mussel bed thickness in the center of the beds away from the edges, which is most comparable to the 50% shore level. In Northern California, at Bodega Bay, Santa Cruz, and Pacific Grove measured bed thicknesses were 16 cm, 8 cm, and 21 cm, respectively. In Southern California at Alegria, Prisoners Harbor, and Willows Anchorage measured bed thicknesses were 5 cm, 6 cm, and 8 cm, respectively. Santa Cruz and Alegria had the thinnest beds compared to other sites within the same geographic region. Santa Cruz and Alegria were also the only two sites in these regions with 100% mortality predicted to occur at the 50% shore level in mussel beds having 5% contact within the bed (Fig. 2a). In order to fully address the winnowing hypothesis, field studies are needed to investigate short-term effects (e.g., percentage of contact of dead mussels relative to live mussels following a heat driven mortality event) and long-term impacts (e.g., the relationship between frequency of heat driven mortality events and bed thickness).

Conductive heat transfer influences the body temperature of other species that live in the intertidal habitat. Greater contact area between littorinid snails and underlying substratum increases snail body temperature on warm, sunny days (Miller and Denny 2011). In contrast, greater contact between top layer mussels and those deeper within the bed decreases mussel body temperature on warm, sunny days (Fig. 3a). The effect of contact area on body temperature is related to the underlying substratum temperature which is determined by shore level and exposure of the substratum to sunlight. Littorinid snails live on bare rock in the high intertidal zone, whereas mussels live on rocks covered with other mussels in the middle and low intertidal zones. Mussels shade the substratum in the middle and low intertidal zones, so the underlying substratum temperature is not influenced by direct solar radiation, and therefore the underlying substratum remains cooler than the overlying macrofauna. Direct solar radiation warms the bare rock in the high intertidal zone, which transfers heat to the littorinid snails (Miller and Denny 2011). In addition, the middle and low intertidal zones are typically covered by high tide at least once per day at which time rock temperature is the same as ocean temperature. The high intertidal zone is less frequently covered by high tide, so the rock temperature is not reset to ocean temperature as often. Therefore, ocean temperature moderates macrofauna and rock temperatures in the middle and low intertidal zones where mussels live but less so in the high intertidal zone where littorinid snails live.

Patchy mortality is observed in other ecosystems after heat waves, and there is some evidence that the patchiness is related to variability in biophysical interactions between organisms and their environment. Coral reefs are among the most prominent examples of patchy mortality (Hughes et al. 2003, Berkelmans et al. 2004). Corals either lose their symbiotic zooxanthellae or reduce photosynthetic pigment concentrations when ocean temperatures are high, causing corals to appear bleached, and bleached corals often die (Glynn 1993, Brown 1997). Bleaching is highly localized and bleached corals are found next to unbleached corals (Hughes et al. 2003, Berkelmans et al. 2004). Mass transfer of oxygen changes over very small spatial scales on reefs and would explain both spatial patchiness of bleaching (Finelli et al. 2007) and the differences in bleaching among corals with different morphologies (van Woesik et al. 2012). Mussel beds and coral reefs provide structural habitat for other species and thus serve to increase biodiversity, but being sessile they are particularly vulnerable to extreme weather conditions. Continuing to identify critical biophysical mechanisms related to mortality and ecological performance will improve our ability to predict the effects of climate change on these vulnerable ecosystems.

ACKNOWLEDGMENTS

K. A. Smith was supported by the NOAA Cooperative Institute for Climate Science (NA08OAR4320752) and the Carbon Mitigation Initiative, which is sponsored by BP. This study was also supported by grants from the NSF (OCE1039513 and OCE1129401), NOAA (NA04NOS4780264), and NASA (NNX07AF20G and NNX11AP77G) to D. S. Wethey. We thank two anonymous reviewers for helpful comments. This is contribution 71 in Ecological Forecasting from the University of South Carolina.

Literature Cited

Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Barron, C. N., and A. B. Kara. 2006. Satellite-based daily SSTs over the global ocean. Geophysical Research Letters 33: L15603.

Berkelmans, R., G. De'ath, S. Kininmonth, and W. J. Skirving. 2004. A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. Coral Reefs 23:74–83.

Brown, B. E. 1997. Coral bleaching: causes and consequences. Coral Reefs 16:S129–S138.

Chawla, A., D. M. Spindler, and H. L. Tolman. 2013. Validation of a thirty year wave hindcast using the Climate Forecast System Reanalysis winds. Ocean Modelling 70:189–206.

Christidis, N., P. A. Stott, S. Brown, G. C. Hegerl, and J. Caesar. 2005. Detection of changes in temperature extremes during the second half of the 20th century. Geophysical Research Letters 32:L20716.

Della-Marta, P. M., M. R. Haylock, J. Luterbacher, and H. Wanner. 2007. Doubled length of western European summer heat waves since 1880. Journal of Geophysical Research: Atmospheres 112:D15103.

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. Journal of Experimental Marine Biology and Ecology 400:175–190.

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

Egbert, G. D., and S. Y. Erofeeva. 2002. Efficient inverse modeling of barotropic ocean tides. Journal of Atmospheric and Oceanic Technology 19:183–204.

Finelli, C. M., B. S. Helmuth, N. D. Pentcheff, and D. S. Wethey. 2007. Intracolony variability in photosynthesis by corals is affected by water flow: role of oxygen flux. Marine Ecology Progress Series 349:103–110.

Fischer, E., and C. Schär. 2010. Consistent geographical patterns of changes in high-impact European heatwaves. Nature Geoscience 3:398–403.

Gates, D. M. 2003. Biophysical ecology. Dover Publications, Mineola, New York, USA.

Glynn, P. W. 1993. Coral reef bleaching: ecological perspectives. Coral Reefs 12:1–17.

Harley, C. D. G. 2008. Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. Marine Ecology Progress Series 371:37–46.

Helmuth, B., B. R. Broitman, C. A. Blanchette, S. Gilman, P. Halpin, C. D. G. Harley, M. J. O'Donnell, G. E. Hofmann, B. Menge, and D. Strickland. 2006. Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. Ecological Monographs 76:461–479.

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., L. Yamane, S. Lalwani, A. Matzelle, A. Tockstein, and N. Gao. 2011. Hidden signals of climate change in intertidal ecosystems: what (not) to expect when you are expecting. Journal of Experimental Marine Biology and Ecology 400:191–199.

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

Hughes, T. P., et al. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933.

McKechnie, A. E., and B. O. Wolf. 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. Biology Letters 6:253–256.

Meehl, G. A., and C. Tebaldi. 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. Science 305:994–997.

Mesinger, F., et al. 2006. North American regional reanalysis. Bulletin of the American Meteorological Society 87:343–360.

Miller, L. P., and M. W. Denny. 2011. Importance of behavior and morphological traits for controlling body temperature in Littorinid snails. Biological Bulletin 220:209–223.

Mislan, K. A. S., B. Helmuth, and D. S. Wethey. 2014. Geographic variation in climatic sensitivity of intertidal mussel zonation. Global Ecology and Biogeography 23:744–756.

Mislan, K. A. S., and D. S. Wethey. 2011. Gridded meteorological data as a resource for mechanistic macroecology in coastal environments. Ecological Applications 21: 2678–2690.

Oswald, E. M., and R. B. Rood. 2014. A trend analysis of the 1930–2010 extreme heat events in the Continental United States. Journal of Applied Meteorology and Climatology 53: 565–582.

Paine, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93–120.

Perkins, S. E., and L. V. Alexander. 2013. On the measurement of heat waves. Journal of Climate 26:4500–4517.

Petes, L. E., B. A. Menge, and G. D. Murphy. 2007. Environmental stress decreases survival, growth, and reproduction in New Zealand mussels. Journal of Experimental Marine Biology and Ecology 351:83–91.

Pinker, R. T., and I. Laszlo. 1992. Modeling surface solar irradiance for satellite applications on a global scale. Journal of Applied Meteorology 31:194–211.

Smith, J. R. 2005. Factors affecting geographic patterns and long-term change of mussel abundances (*Mytilus californianus* Conrad) and bed-associated community composition along the California coast. Dissertation. University of California, Los Angeles, California, USA.

Suchanek, T. H. 1978. The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. Journal of Experimental Marine Biology and Ecology 31:105–120.

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.

Tsuchiya, M. 1983. Mass mortality in a population of the mussel *Mytilus edulis* L. caused by high temperature on rocky shores. Journal of Experimental Marine Biology and Ecology 66:101–111.

U.S. Army Corps of Engineers. 2002. Coastal engineering manual. U.S. Army Corps of Engineers, Washington, D.C, USA.

van Woesik, R., A. Irikawa, R. Anzai, and T. Nakamura. 2012. Effects of coral colony morphologies on mass transfer and susceptibility to thermal stress. Coral Reefs 31:633–639.

Wethey, D. S. 1983. Geographic limits and local zonation: the barnacles *Semibalanus* (*Balanus*) and *Chthamalus* in New England. Biological Bulletin 165:330–341.

Wethey, D. S. 1984. Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*: a field experiment. Biological Bulletin 167:176–185.

Wethey, D. S., L. D. Brin, B. Helmuth, and K. A. S. Mislan. 2011. Predicting intertidal organism temperatures with modified land surface models. Ecological Modelling 222: 3568–3576.

Supplemental Material

Data Availability

Code associated with this paper has been deposited in Zenodo: http://dx.doi.org/10.5281/zenodo.13380