
VOL. 400, NOS. 1–2
30 APRIL 2011
ISSN 0022-0981
ELSEVIER
Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY
Special Issue
Global Change in Marine Ecosystems
Guest Editors
Stephen J. Hawkins
Louise B. Firth

Journal of Experimental Marine Biology and Ecology 400 (2011) 209–217

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

# Geographic variation in temperature tolerance as an indicator of potential population responses to climate change

Cascade J.B. Sorte [a,*], Sierra J. Jones [b], Luke P. Miller [a]

[a] Marine Science Center, Northeastern University, Nahant, MA 01908, USA
[b] Department of Biological Sciences, University of South Carolina, Columbia, SC 29208, USA

ARTICLE INFO

*Keywords:*
Acclimatization
Biogeography
Climate change
Ecological forecasting
Ecophysiology
Temperature tolerance

## ABSTRACT

The temperature tolerances of individuals in geographically separated populations of a single species can be used as indicators of each population's potential to persist or become extinct in response to climate change. We evaluated the population-level variation in temperature tolerance in populations of several marine invertebrate taxa, including bryozoans, tunicates, bivalves, and gastropods, separated by distances of <200 km to >5000 km. We then combined physiological thermotolerance data with current temperature data and climate change predictions to predict which of these populations may be most vulnerable to future changes. In a trans-continental comparison of four subtidal epibenthic species, we show that populations on the east coast of the United States, which experienced higher habitat temperatures than those on the west coast, had higher thermal tolerances but lived closer to individuals' tolerance limits. Similarly, temperature tolerances varied between western and eastern Atlantic populations of the mussel *Mytilus edulis*; however, these differences only emerged after repeated exposures to high temperatures. Furthermore, the less thermotolerant *M. edulis* population in the western Atlantic was more susceptible to temperature increases, as evidenced by a recent range contraction. Thus, for both the subtidal epibenthic and intertidal mussel species, we identified the western Atlantic as a 'hot spot' of populations susceptible to climate change compared to those in the eastern Pacific and eastern Atlantic, respectively. Finally, because current tolerances are not the sole indicators of individuals' abilities to cope with temperature increases, we also assessed the possibility for acclimatization to facilitate the persistence of populations *via* the buffering of temperature effects. We show that, for four populations of intertidal *Littorina* snail species in the northwest Atlantic, most populations were able to overcome geographic differences in temperature tolerance *via* acclimation. When acclimation capacity is low, the potential for "rescue" may depend on the particular species' life-history strategy and dispersal ability. For example, although individuals from the coldest-adapted population of *Littorina littorea* were unable to acclimate as quickly as those from more southern populations, this species has a pelagic larval stage and, thus, the greatest dispersal potential of these littorines. Together, these studies highlight the importance of considering variation in temperature tolerance between populations within species to improve the forecasting of changes in the abundances and distributions of species in response to climate warming.

## 1. Introduction

As mean and extreme temperatures increase in marine systems, the likelihood that a given population persists is partly related to the physiological capacity of organisms to tolerate elevated temperatures (Hutchins, 1947; Newell, 1969, 1979). Temperature clearly affects species' distribution patterns: a strong relationship between upper temperature tolerance and maximum habitat temperature has been demonstrated for many species (Wolcott, 1973; Tomanek and Somero, 1999; Stillman and Somero, 2000; Stillman, 2002; Wethey, 2002; Miller et al., 2009; Lockwood and Somero, 2011-this issue). Shifts in species' ranges have been linked to rising mean temperatures (Southward et al., 1995; Herbert et al., 2003; Mieszkowska et al., 2005; Helmuth et al., 2006; Wethey and Woodin, 2008; Sorte et al., 2010a; Poloczanska et al., 2011-this issue). Furthermore, increases in extreme temperatures have been followed by mortality events (Garrabou et al., 2009; Firth and Williams, 2009; Jones et al., 2009, 2010; Marbà and Duarte, 2010). Recent studies have focused on interspecific differences in temperature tolerance – particularly between closely related congeners – to identify organismal and ecological characteristics of the "winners" and "losers" of climate change (Somero, 2010). It has been suggested that species with higher temperature tolerances will be better able to cope with global warming (Calosi et al., 2008) or, conversely, that more warm-adapted species will be at a disadvantage because they tend to live closer to

---

* Corresponding author at: Marine Science Center, Northeastern Univ., 430 Nahant Road, Nahant, MA 01908, USA. Tel.: +1 781 581 7370x328; fax: +1 781 581 6076.
*E-mail addresses:* cjsorte@ucdavis.edu (C.J.B. Sorte), sierra.jenell.jones@gmail.com (S.J. Jones), contact@lukemiller.org (L.P. Miller).

doi:10.1016/j.jembe.2011.02.009

their absolute tolerance limits (Stillman and Somero, 2000; Somero, 2005, 2010; Compton et al., 2007; Bonebrake and Mastrandrea, 2010) and have lower acclimation potentials (Stillman, 2003; Somero, 2005; Stenseng et al., 2005; Ghalambor et al., 2006). In this paper, we treat these hypotheses by taking a more intimate look at geographic variation in temperature tolerance *within* species, including its potential as an indicator of regions likely to experience local extinction or population persistence.

Geographic variation in temperature tolerance, or differences in the average individual tolerances between geographically distinct populations, arises due to individual variation. This variation in temperature tolerance of an organism represents both adaptation (a distinct genotype) and phenotypic plasticity, or the range of phenotypes possible for a single genotype, which can be either fixed or variable over an individual's lifespan. Most studies examining geographic variation in thermal tolerance have focused on differences along a latitudinal gradient, including studies designed to test and explain Rapoport's rule (that latitudinal range size increases with latitude; Addo-Bediako et al., 2000) and Janzen's hypothesis (that mountain passes – as abrupt environmental breaks – are physiologically 'higher' for stenothermal, warm-adapted tropical species; Janzen, 1967; Ghalambor et al., 2006). At the species level, latitudinal distribution is often positively related to thermal tolerance range, although the implications for responses to climate change are equivocal given that this pattern is often driven by greater variation in lower, rather than upper, tolerance limits (Goto and Kimura, 1998; Gaston and Chown, 1999; Addo-Bediako et al., 2000; Kimura, 2004).

Here, we consider geographic variation in the upper limit of temperature tolerance in the context of predicting population-level responses to climate change. Populations which are likely to persist in the warmer conditions predicted with climate change are those in which, as diagrammed in Fig. 1: (i) individuals have high temperature tolerances, (ii) individuals have the capacity, *via* phenotypic plasticity, to acclimate to higher temperatures, or (iii) populations of tolerant individuals – those that either already have high tolerance or have high acclimatization capacity – can disperse and re-seed areas of less tolerant populations (Deutsch et al., 2008). Thus, populations that are more prone to local extinction will be those in which individuals have low temperature tolerance, low acclimatization capacity, and/or low dispersal ability (Deutsch et al., 2008). We present three case studies in which we combine physiological thermotolerance data with current temperature data and climate change predictions. By examining ecophysiological and biogeographic patterns for a diverse set of marine taxa – including bryozoans, tunicates, bivalves, and gastropods – we provide a starting point for addressing broad questions about climate-change impacts relevant to many systems, both marine and terrestrial, such as:

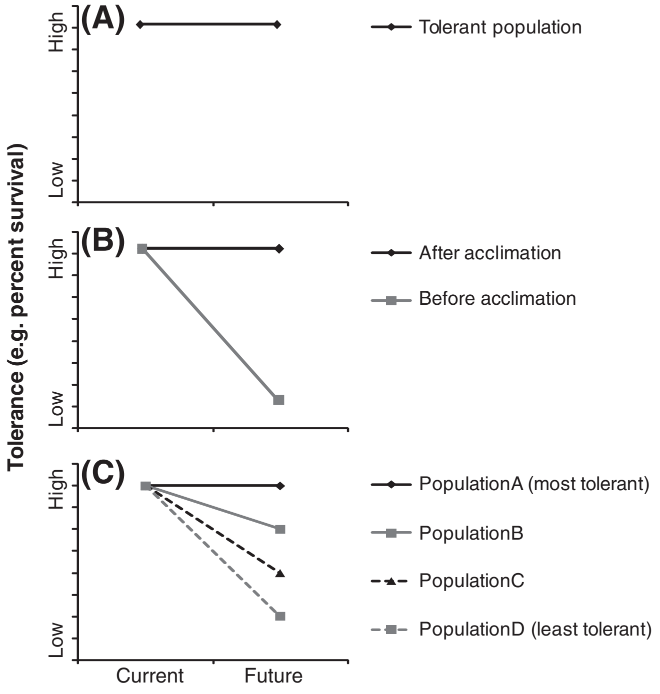

**Fig. 1.** Conceptual diagram of three methods that could allow population persistence in future climate conditions. (A) If future conditions are within the local population's current tolerance range, then survival will continue to be high. (B) If future conditions are within the range of acclimation capacity for this local population, then survival might be low before acclimation but high after acclimation. (C) If tolerance varies between populations connected *via* dispersal, then individuals from more tolerant source populations could recolonize areas of high mortality (i.e. with less tolerant local populations).

(1) How do temperature tolerances vary geographically over small (i.e. regional) and large (i.e. trans-continental and trans-oceanic) scales?
(2) Are populations with higher average temperature tolerances likely to be at an advantage due to their capability of surviving at increased temperatures or at a disadvantage due to a narrower distance between their tolerance limits and projected temperature exposures?
(3) Do more tolerant populations possess the acclimation capacity and dispersal potential that could "rescue" vulnerable populations from local extinction?

## 2. Epibenthic fouling species: a trans-continental comparison

Populations separated by continents or ocean basins exchange propagules only rarely and may, thus, exhibit a marked variation in acclimatization and adaptation of temperature tolerance (e.g. see Vellend et al., 2007). We determined the upper $LT_{50}$, or temperature lethal to 50% of individuals in the population, for four epibenthic species collected in Massachusetts (USA; on the east coast) and compared these values to those for individuals collected in California (USA; on the west coast).

### 2.1. Methods

In July and August 2010, four epibenthic species settled naturally onto plastic tiles (Duplos; LEGO Group, Billund, Denmark) deployed in marinas at approx. 1 m depth. The tunicates *Botrylloides violaceus* and *Botryllus schlosseri* were collected on tiles deployed at Lynn, Massachusetts (42.4577°N, 70.9434°W), and the tunicate *Diplosoma listerianum* and bryozoan *Bugula neritina* were similarly obtained at Hawthorne Cove Marina in Salem, Massachusetts (42.5195°N, 70.8872°W). West coast individuals were collected at Bodega Harbor, California (38.3311°N, 123.0567°W) in July and August 2009.

Lethal temperatures in east coast populations were determined following the methods detailed in Sorte et al. (2010b) with exceptions as noted below. Briefly, individuals were acclimated in the laboratory in running seawater at ambient temperature (approx. 17 °C) for 24 h, after which tiles containing 2 individuals (colonies) of a single species were placed in separate 1 L experimental chambers (note: one individual per chamber was used for *B. neritina* when necessary due to low recruitment). Temperature was raised at a rate of 1 °C/5 min until the treatment temperature was reached, and mortality was assessed following a 24 h temperature exposure (at approx. 21, 25, 29, and 34 °C; actual chamber temperatures were used in the analyses). $LT_{50}$ values were calculated by Probit analysis in SAS v 9.1 (SAS Institute, Cary, North Carolina, USA) and were compared to values for west coast populations determined in July and August 2009 (Zerebecki and Sorte, in press).

Projected temperature changes for the east and west coast sites studied were calculated from nine global circulation models available

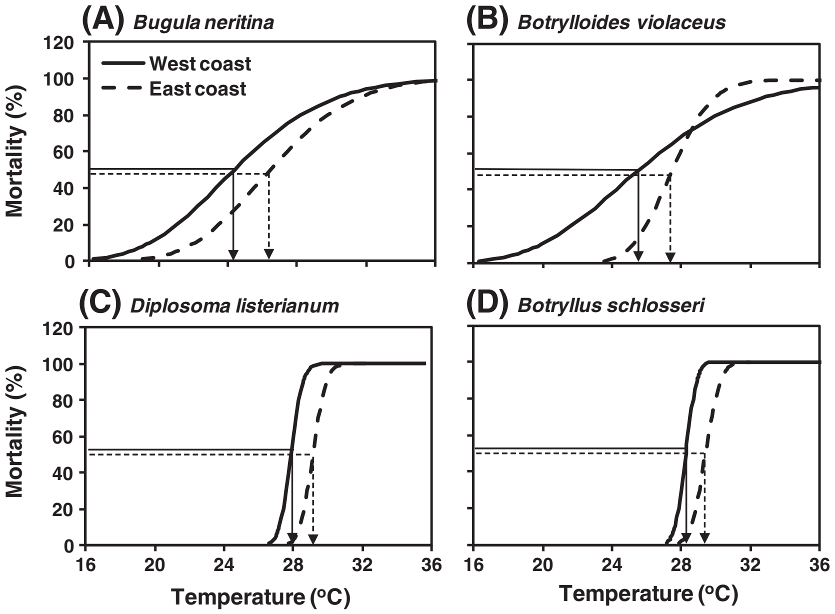

**Fig. 2.** Temperature-dependent mortality predicted by Probit analysis for (A) the bryozoan *Bugula neritina*, and the tunicates (B) *Botrylloides violaceus*, (C) *Diplosoma listerianum*, and (D) *Botryllus schlosseri* from the USA west coast (California) and east coast (Massachusetts). For all four species, $LT_{50}$ was higher on the east coast than on the west coast. Values are based on mortality following a 24 h exposure to four experimental temperatures (approx. 21, 25, 29, and 34 °C). Replication was as follows: *B. violaceus* and *B. schlosseri*: $n = 5$ per temperature; *B. neritina*: $n = 7$, 8, 1, and 4, respectively; and *D. listerianum*: $n = 3$, 2, 9, and 6, respectively.

as part of the World Climate Research Programme's Coupled Model Intercomparison Project 3 (CMIP3; Meehl et al., 2007). We calculated the changes in average monthly sea surface temperatures using the Intergovernmental Panel on Climate Change SRES A1B emissions scenario (IPCC Working Group III, 2000). Data from each climate model were processed in the program R v 2.11.1 (R Core Development Team, 2010) to extract the projected average monthly temperatures for the ocean grid cell closest to each of our sites. We used temperature estimates from 1961 to 1990 as the baseline for comparison against the future projections for 2090–99. We calculated the mean temperature in each time period (1961–90 and 2090–99) separately for each month (January–December) and used the difference between the two time periods as our estimate of future temperature change for each month of the year. The average temperature change for the entire year was calculated from the monthly changes.

### 2.2. Results and discussion

Lethal temperatures were higher for east coast than west coast populations of all four epibenthic species (1-sample *t*-test: $t = 6.1207$, $df = 3$, $p = 0.0088$; Fig. 2). The difference between $LT_{50}$ values for east and west coast populations ranged from 1.1 °C for *B. schlosseri* to 2.1 °C for *B. violaceus*. Absolute $LT_{50}$ values (east/west coast) were 29.4/28.3 °C for *B. schlosseri*, 27.4/25.3 °C for *B. violaceus*, 29.1/27.9 °C for *D. listerianum*, and 26.4/24.4 °C for *B. neritina*. The magnitude of variation in temperature tolerance between east and west coast populations was strongly related to the $LT_{50}$: species that were *less* thermotolerant on the west coast displayed a *greater difference* in $LT_{50}$ between the east and west coasts ($F_{1,2} = 25.92$, $p = 0.0365$; $R^2 = 0.93$).

Temperature tolerances also paralleled habitat temperatures. Mean summertime water temperature in Massachusetts was 2.4 °C warmer than in California (June–August, 2006–2010), and annual temperature range was twice as broad – 24.9 *versus* 12.4 °C – in the eastern USA (Fig. 3; Sorte and Stachowicz, in review; MA data from NOAA National Buoy Data Center <www.nbdc.noaa.gov> Boston Harbor station BHB3M). The east coast populations are currently living closer to individuals' summer tolerance limits: maximum summertime temperatures were 4.4 °C higher in Massachusetts, and these local temperature maxima were within 3.9 °C of the populations' $LT_{50}$ values on the east coast but 6.7 °C below those on the west coast. The species living closest to its tolerance limit, the bryozoan *B. neritina*, encountered maximum temperatures within 2.2 °C and 4.6 °C of its $LT_{50}$ on the east and west coasts, respectively.

If acclimatization and adaptation abilities do not vary between populations, then the east coast populations will continue to be more susceptible due to expected increases in ocean temperatures. When projected temperature increases are taken into account, summer (June–August) sea surface temperatures on the east coast are likely to approach or exceed the $LT_{50}$ values of the two species living closest to their tolerance limits, *B. neritina* and *B. violaceus*, by the end of the 21st century. In Massachusetts, mean summer and annual sea surface temperatures are projected to rise by 3.0 and 3.3 °C, respectively. In California, mean increases of 2.4 and 2.7 °C are predicted for summer and annual sea surface temperatures, respectively, which are still

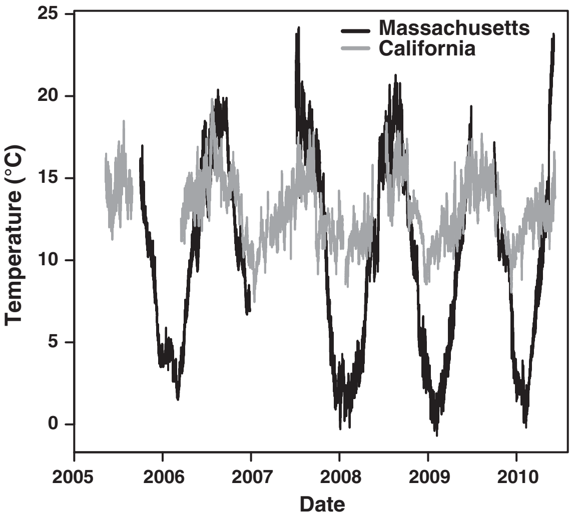

**Fig. 3.** Water temperatures from Boston Harbor, Massachusetts (on the USA east coast; black line) and Bodega Harbor, California (on the USA west coast; gray line) for 2005–10.

below the four species' $LT_{50}$ values. However, for California populations of *B. neritina* and *B. violaceus*, this increase in summer temperatures could nevertheless elicit 20–30% mortality (Fig. 2).

These data support, at the population level, the documented pattern that species living at higher temperatures occur closer to their absolute tolerance limits (i.e. Stillman and Somero, 2000; Somero, 2005, 2010; Compton et al., 2007; Deutsch et al., 2008), and they suggest that east coast populations will be at a disadvantage in warmer conditions relative to west coast populations. This prediction, however, neglects these species' potentials for acclimatization and local adaptation, which may, if representative of genotypic variation, be indicated by two studies showing significant phenotypic variation over small distances. For example, Grosholz (2001) showed local adaptation in minimum temperature tolerance of *Botrylloides* sp. between sites separated by <60 km, and variation in habitat temperatures may have caused differences in *B. schlosseri* population dynamics between sites only <20 km distant (Yund and Stires, 2002). Such fine-scale population adaptation is possible for species that lack a pelagic larval stage and recruit extremely locally, such as the intertidal dogwhelk *Nucella canaliculata* (Kuo and Sanford, 2009) and the four epibenthic species treated here. Clearly, these epibenthic species have the potential for acclimatization and/or rapid local adaptation: all four are non-natives that were most, if not all, introduced to California during the past century (Cohen, 2005), and already there are apparent differences in temperature tolerance between east and west coast populations. Interestingly, the two least tolerant species also showed the greatest individual variation in temperature tolerance (as indicated by the shallower slope of their tolerance curves in Fig. 2) suggesting – if phenotypic variation indicates genotypic variation – that populations of these species have a greater potential for adaptation.

A comparison with previous research in the Bodega Harbor epibenthic community showed strong effects of age on survival rate and that the impacts of increased temperatures can be exacerbated – and even reversed – in older individuals. For example, a 3-day experimental heat wave of 24.5 °C caused 100% mortality in adults of the three tunicate species considered here but little to no mortality in adults of the bryozoan *B. neritina* (Sorte et al., 2010c), which is the most susceptible of these species as a juvenile. Furthermore, on the west coast, $LT_{50}$ values were lower for native species than for non-native species overall (Sorte et al., 2010b). Thus, both on the east and west coasts, different life stages, and the respective suite of native species, may be living more 'on the edge' in epibenthic communities.

## 3. Marine mussels: a cross-ocean comparison

Compared to the shallow subtidal systems discussed above, where temperatures vary by <25 °C annually and less on shorter (i.e. daily) timescales, the marine intertidal zone is a physically rigorous habitat in which rapid and extreme fluctuations in temperature occur on a daily basis. Mussels in the genus *Mytilus* are major space occupiers of marine intertidal habitats, and, like tunicates and bryozoans, are sedentary. Because their responses to environmental change are largely unmitigated by behavior, their upper intertidal and equatorward geographic distributions are often constrained by physiological limits, such as thermal tolerance.

### 3.1. Methods

The upper thermal tolerance of the mussel *Mytilus edulis* was determined for western and eastern Atlantic populations using the methods presented in Jones et al. (2009). Adult mussels were collected from Nahant, Massachusetts, USA (42.4195°N, 70.9023°W) on 20 June 2006 and from Luc-sur-Mer, Normandy, France (49.3110°N, 0.3555°W) on 5 July 2010. Shell lengths (mean ± SD) were 45.2 ± 5.0 mm and 27.14 ± 2.15 mm for the mussels from the USA and France (FR), respectively. Upon collection, the animals were transported in coolers to temperature-controlled recirculating seawater tanks ("control" tanks: Living Streams; Frigid Units, Toledo, Ohio, USA) with a semidiurnal tidal cycle at the University of South Carolina (Columbia, South Carolina, USA) and acclimated for 1 week.

Water temperature in the control tanks was maintained at approximate ambient field temperatures of 18 °C (USA) and 19 °C (FR) for the duration of the experiment. Most thermal tolerance experiments previously conducted on *M. edulis* examined the response to water temperatures alone (Ritchie, 1927; Read and Cumming, 1967; Pearce, 1969; Rajagopal et al., 2005). However, because these intertidal mussels are exposed to both submerged and aerial conditions, each experimental trial was run in both water and air at a range of environmentally realistic temperatures, including 25, 30, 32.5, 35, and 40 °C, with three replicates of 5 animals for each temperature treatment ($n = 15$ per temperature × medium treatment). Reach-in incubators were maintained for the duration of the experiment at each of the target temperatures to within ± 0.25 °C. Aquaria (38 L) were placed inside the incubators, and in this manner both the air and water treatments could be run simultaneously. The role of evaporative cooling in mussels (i.e. gaping) was assumed to be negligible, as Fitzhenry et al. (2004) showed that mussel body temperatures were not related to gaping ability.

Mussels were exposed to the same temperature for a 6 h period each day, simulating one tidal event per day, and the experiment was run for 5 consecutive days as a means of discerning the effects of thermal history. Following each exposure event, mussels were removed from the incubators and returned to the respective control tanks (with tidal period) for a recovery period of 18 h, after which we counted the numbers of dead individuals. The recovery period simulated natural conditions in which a period of stress is followed by an extended period of immersion and/or a second emersion during the morning or night when air temperatures are relatively low. Mussels from the air and water treatments were held in separate control tanks on opposing tidal cycles in order to ensure proper cycling of emersion and immersion periods. The $LT_{50}$ values were calculated for each exposure event by linear interpolation of the graphs of cumulative survival *versus* temperature in R v 2.8.1 (R Core Development Team, 2010).

### 3.2. Results and discussion

Multiple exposures decreased temperature tolerances for both the USA and French populations of *M. edulis* (Fig. 4). For both populations, there was a fast initial decline in tolerance, and tolerance tended to plateau after the third exposure. The two populations tended to diverge after the second exposure, and population differences in $LT_{50}$ continued to increase through the fifth exposure. By the fifth

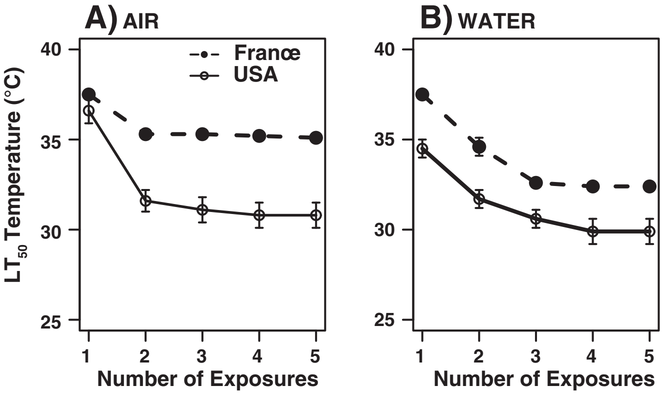

**Fig. 4.** Calculated $LT_{50}$ values (± 1 SE) for *Mytilus edulis* after five consecutive exposure events in (A) air and (B) water. Mussels were collected from Normandy, France (dashed line, closed circles) and Massachusetts, USA (solid line, open circles).

exposure, mussels from the French population of *M. edulis* had thermal tolerances that exceeded those from the USA population by 4.5 °C and 2.5 °C in air and water, respectively. Thus, there was a common relationship between $LT_{50}$ and the number of exposures for both populations, with thermal tolerance decreasing as a function of increasing exposures. These findings indicate the importance of accounting for thermal history when examining survival within an ecological context.

When $LT_{50}$ values were averaged across the 5 exposures, tolerances were higher for FR than USA mussels in both air (Welch Two-Sample *t*-test; $t=2.776$, $df=5.109$, $p=0.038$) and water (Welch Two-Sample *t*-test; $t=1.966$, $df=7.846$, $p=0.086$). However, in this cross-ocean comparison of *M. edulis*, differences in temperature tolerances did not parallel those in habitat temperatures. Daily optimally interpolated sea surface temperature (OISST) data on a 0.25° grid (Reynolds et al., 2007) were obtained for the nearest pixel corresponding with collection sites for the period January 1998–December 2008. There was little to no difference between USA and FR locations in annual maximum ocean temperatures, which ranged from 19.6 to 22.7 °C in FR, with an average maximum of 20.8 °C, and between 19.3 and 21.3 °C in the USA, with an average maximum of 20.7 °C. Considering that an immersed mussel will have the same body temperature as the water (Gilman et al., 2006), the differences in immersed thermal tolerances between the two populations are surprising since maximum habitat water temperatures are similar. Interestingly, the seasonal range in temperatures experienced was, on average, 4.3 °C greater in the USA/western Atlantic where the population is composed of less thermally tolerant individuals.

The disconnection between habitat temperatures and thermal tolerances was even more pronounced for air temperatures. Hourly air temperature data were obtained from the National Climatic Data Center (www.ncdc.noaa.gov) for Boston, Massachusetts, USA (42.3584°N, 71.0598°W; Site ID: 725090) and Cap de la Hève, France (49.5167°N, 0.0667°E; Site ID: 070280) for the period January 1998–December 2009. Annual average maximum temperature for FR ranged between 29.4 and 36.1 °C, with an average maximum of 31.2 °C, while the range for the USA was 33.3–37.8 °C, with an average maximum of 35.2 °C. As with sea surface temperatures, the seasonal range in air temperature was much greater for the western Atlantic population: 50.8 °C in the USA *versus* 35.6 °C in the eastern Atlantic. The disparity between tolerance and habitat temperatures could partially reflect the fact that while emerged at low tide, the body temperature of a mussel may be higher than the ambient air temperature (Hofmann and Somero, 1995; Denny et al., 2011-this issue). However, overall, the suggestion that more warm-adapted species tend to live closer to their thermal tolerance limits (Stillman and Somero, 2000; Somero, 2005, 2010; Compton et al., 2007; Bonebrake and Mastrandrea, 2010) does not appear to be the case for these mussel populations. The population with the highest thermal tolerances (FR) experienced cooler temperatures and a narrower seasonal temperature range whereas mussels in the population with lower thermal tolerances (USA) inhabited locations with higher maximum habitat temperatures and a broader temperature range.

Repeated, chronic exposures to high temperatures have been demonstrated to have negative effects on a variety of organisms, impacting foraging behavior in the marine intertidal seastar *Pisaster ochraceus* (Pincebourde et al., 2008), growth of the benthic stream minnow *Rhinichthys cobitis* (Widmer et al., 2006), and fecundity and viability in the fruit fly *Drosophila melanogaster* (Dillon et al., 2007). A decrease in upper thermal tolerance after repeated exposures has been observed in other mussel species, including *Mytilus trossulus*, *Mytilus galloprovincialis*, and *Mytilus californianus*, from the west coast of the USA (S. Jones and N. Mieszkowska, unpubl. data), in addition to that shown here for *M. edulis* from the Atlantic. While the physiological mechanisms underlying these results are unknown, we suggest that they could reflect costs associated with sublethal stress, such as the expression of heat-shock proteins. Hilbish et al. (unpubl. data) determined that the threshold induction temperature of the heat-shock response for *M. edulis* from the USA was between 29 and 32 °C, which is very close to the $LT_{50}$ values derived from the temperature tolerance experiments. Repeated exposures to such high temperatures may override the heat-shock response: Chapple et al. (1998) found that *M. edulis* could not acclimate to temperatures above 28.5 °C, and Hilbish et al. (unpubl. data) showed that heat-shock protein expression increased with temperatures up to 32 °C but declined dramatically at 35 °C. These data indicate that the heat-shock response may not be able to compensate for repeated exposures to high temperatures, increasing the probability of mortality with more frequent heat exposure.

Many intertidal organisms tend to live at the limits of their temperature tolerances, both within the intertidal zone and on a geographic scale (Connell, 1961, 1972; Wolcott, 1973; Newell, 1979; Wethey, 2002; Jones et al., 2009), and *Mytilus* is no exception. Analysis of intertidal temperature records for the east coast of the USA and northern Europe indicated that between two and five consecutive daily exposures to high temperatures typically occur during a spring tidal cycle (S. Jones, unpubl. data; B. Helmuth and N. Mieszkowska, unpubl. data). As a result, high mortality in response to these repeated exposures has been documented (Jones et al., 2010). Increases in ambient temperature due to climatic change, and increases in the frequency of heat waves, could therefore affect both small- and large-scale distributions. For *M. edulis* along the western Atlantic, a range contraction of approximately 350 km in response to rising temperatures has already been documented (Jones et al., 2010). However, such a change in distribution has not been seen for *M. edulis* along the eastern Atlantic (Wethey et al., 2011-this volume), which could be due to the fact that temperature tolerances in northern France are much higher than those on the USA east coast.

## 4. Within-region variation in northwest Atlantic littorine snails

Repeated exposure to temperature change in the long term, however, may allow acclimatization, which can protect populations from extreme temperature and mortality episodes. We determined the temperature tolerance of littorine snail congeners along a latitudinal and temperature gradient in the northwest Atlantic to assess within-region variation in tolerance, and two lab-acclimation treatments allowed examination of relative acclimatization and acclimation ability.

### 4.1. Methods

Individuals of three *Littorina* species – *Littorina littorea*, *Littorina obtusata*, and *Littorina saxatilis* – were collected between 19 July and 11 August 2010 from four locations in the northeastern USA: northern Maine (Hamilton Cove, near Quoddy Head; 44.7867°N, 67.0064°W), southern Maine (Pemaquid Point; 43.8406°N, 69.5098°W), Massachusetts (East Point, Nahant; 42.4195°N, 70.9023°W), and Rhode Island (Kings Beach; 41.3856°N, 71.6639°W; except that no *L. saxatilis* were collected from this site). Individuals were kept in the laboratory with running seawater at 17 °C for acclimation periods of either 5 days or 3 weeks with $n=12$ per species × site × acclimation time. Snails acclimated for 3 weeks were fed *ad libitum* with the alga *Fucus vesiculosis*, replaced twice per week.

Temperature tolerance (emersed, at 100% humidity) was quantified using methods detailed in Sorte and Hofmann (2005), with exceptions as noted. We raised the temperature in experimental vials to 40 °C at a rate of 1 °C every 5 min, exposed the snails to 40 °C for 1 h, and returned the snails to ambient, running seawater for a 90 min recovery period. Tolerance was scored based on responsiveness to probing according to Bertness and Schneider (1976): 0 = dead, no response; 1 = moribund, slight response indicating a compromised ability to reattach to the substrate and, thus, potential mortality *via* wave displacement; and 2 = alive, responsive to probing. These values were averaged across replicates to obtain a thermotolerance index ranging from 0.0 (low) to 2.0 (high). Geographic variation in temperature tolerance (log-transformed values) was assessed by ANCOVA using snail size (measured as operculum width) as the covariate. The size*site interaction was not included in the model when slopes were homogeneous. We ran a separate ANCOVA for each species × acclimation group and used least-squares means for multiple comparisons. We examined residual plots to ensure that the data met the requirements of normality and homogeneity of variances, and we present all data as means ± SE.

### 4.2. Results and discussion

Temperature tolerance varied geographically between field-acclimatized (5-day acclimated) populations of *L. obtusata* (site $F_{3,44} = 9.08$, $p < 0.0001$) and *L. saxatilis* (site $F_{2,32} = 4.66$, $p = 0.017$). For the low to mid-intertidal littorines, *L. littorea* and *L. obtusata*, temperature tolerance of field-acclimatized individuals was highest in the Rhode Island population (i.e. the warmest site) and lowest in the Maine populations (Fig. 5). *L. littorea* tolerances tended to increase monotonically with decreasing latitude (site $p = 0.103$) whereas *L. obtusata* tolerances were lowest in the southern Maine population ($p < 0.0001$). Interestingly, for the high intertidal species *L. saxatilis*, tolerance was highest at the northern Maine location ($p = 0.017$), although, since this species was not collected at the warmest Rhode Island site, our latitudinal comparison was more limited. Thus, these *Littorina* species tend to have less tolerant phenotypes north of Cape Cod, a biogeographic barrier between different thermal habitats (Engle and Summers, 1999; Fig. 5A). At the same time, our comparisons indicate that differences between sites separated by <200 km (e.g. *L. obtusata* in southern *versus* northern Maine) can be as significant as, or greater than, those between sites with >500 km geographic separation. Similarly, Davenport and Davenport (2005) showed that within a suite of 10 rocky intertidal species, differences in thermal niche widths were often the same or greater between sites within a single region than between multiple regions (but see Fangue et al., 2006 for an example of a species with tolerance variation only between, but not within, regions).

Temperature tolerances tended to increase after 3 weeks of laboratory acclimation for all 11 populations examined (Fig. 5A). However, the effect of the acclimation period on the degree of geographic variation in temperature tolerance between populations differed by species. For *L. obtusata* and *L. saxatilis*, the significant geographic variation in tolerance disappeared (*L. obtusata*: site $p > 0.2$) or was obscured (*L. saxatilis*: site $p = 0.062$) after the acclimation period. Conversely, for *L. littorea*, the geographic variation became more pronounced after acclimation (site $F_{3,40} = 4.09$, $p = 0.0127$), with the acclimation capacity of the northern Maine snails lagging behind that of the more southern populations. Among these 11 populations of littorine snails, only two populations – *L. littorea* from northern Maine and *L. saxatilis* from southern Maine – were unable to 'keep up with' their southern counterparts that were more tolerant and better able to acclimate (Fig. 5). Of these species, *L. littorea*, which releases eggs that hatch into pelagic larvae, has a greater ability for more tolerant populations to recolonize and 'rescue' less tolerant populations than the other two direct-developing species that have shorter dispersal distances (Reid, 1996).

Among these three littorines, *L. obtusata*, while able to acclimate to increased temperature, had tolerance levels that were still well below those of the other species. Average tolerance scores for *L. obtusata* were 1.2 ± 0.2 for both Maine populations after the acclimation period, or slightly higher than 'moribund' (a score of 1) which Bertness and Schneider (1976) suggested is approximately the point of 50% mortality. Even if some populations manage to acclimatize sufficiently to avoid high mortality (e.g. the Rhode Island population achieved a tolerance

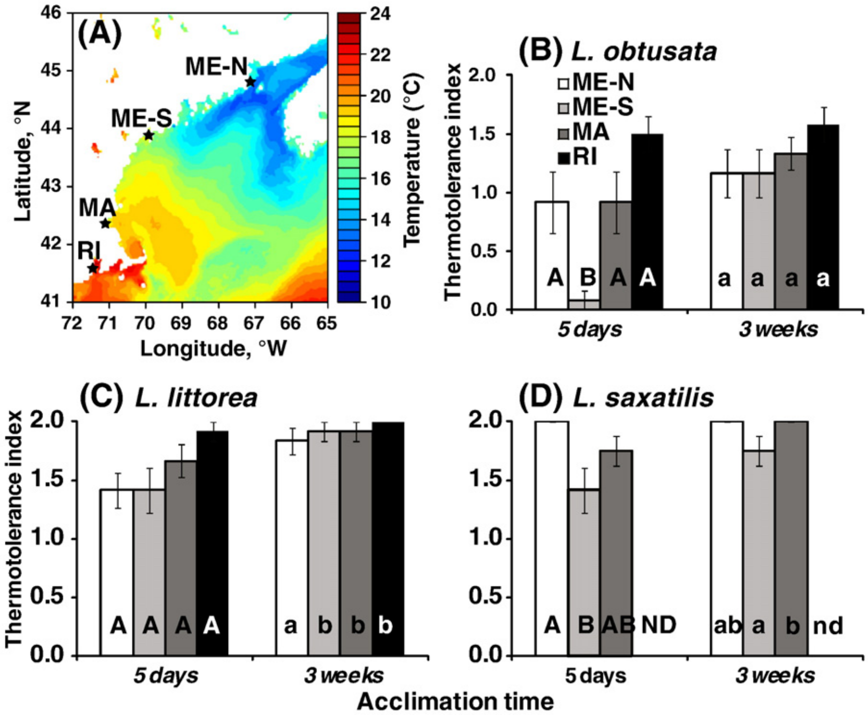

**Fig. 5.** Collection locations (A) and thermal tolerances (B–D) of intertidal *Littorina* snails from the northwestern Atlantic, USA, including (B) *L. obtusata*, (C) *L. littorea*, and (D) *L. saxatilis*. Mean sea surface temperatures (A) across the sampling locations were derived from MODIS-Aqua satellite data for 1-July through 31-August (2002–10). Individual snails ($n = 12$) were collected at Quoddy Head, Maine (ME-N); Pemaquid Point, Maine (ME-S); Nahant, Massachusetts (MA); and Kings Beach, Rhode Island (RI). Snails were lab acclimated for 5 days and 3 weeks to assess field tolerance and acclimation ability, respectively. Thermotolerance was scored (see '4.1 Methods') after a 24 hour emersed exposure to 40 °C using the following indices: 0 = dead, 1 = moribund, and 2 = alive. Different letters indicate significant geographic variation in tolerance within each species × acclimation group (ND = no data). Values are means ± 1 SE.

score of 1.6 ± 0.2 after the 3 week acclimation), dispersal distance is low due to this species' life-history strategy. However, *L. obtusata* are also often found among the blades of their fucoid algal food source (C. Sorte, unpubl. data) which could provide a temperature refuge. Thus, for littorines as well as other marine species, microhabitat buffering (i.e. movement into nearby algal canopies, rock crevices, and cracks) and other behavioral responses (e.g., Williams et al., 2005; Miller, 2008) could ameliorate stressful exposures (Williams et al., 2008). Overall, this case study illustrates the need to consider acclimatization capacity when attempting to project population- and species-level responses to climate change, and future studies exploring the role of dispersal ability and behavioral responses are warranted.

## 5. Overview

The geographic distribution of a species tends to be closely linked with climate, and understanding that relationship is imperative when predicting impacts of climatic change. Hutchins (1947) argued that geographic limits are set by thermal tolerances, and in many cases correspondences have been demonstrated between geographic and physiological limits (e.g. Vernberg and Vernberg, 1967; Sorte and Hofmann, 2005; Jones et al., 2009; Somero, 2010). Marine ectotherms, such as tunicates, bryozoans, bivalves, and gastropods, may be particularly sensitive indicators of climate change (Somero, 2002; Mieszkowska et al., 2005; Helmuth et al., 2006). While studies of species-specific temperature tolerance are relatively common, fewer data are available regarding how tolerances vary on a geographic scale between populations within a single species (O'Neill et al., 2008; Kuo and Sanford, 2009; but see e.g. Urban, 1994; Zippay and Hofmann, 2010).

We examined the variation in thermal tolerances between widely geographically separated populations within species of tunicates (*D. listerianum*, *B. violaceus*, and *B. schlosseri*), bryozoans (*B. neritina*), and bivalves (*M. edulis*). Contrary to some previous findings (e.g. Goto and Kimura, 1998; Gaston and Chown, 1999; Addo-Bediako et al., 2000; Kimura, 2004), our results indicate that upper thermal thresholds do vary between geographically separated populations. Among the subtidal tunicates and bryozoans, differences in $LT_{50}$ values ranged from 1.1 to 2.1 °C between the west and east coast USA populations, and, in each case, tolerance was significantly greater for populations on the east coast. Upper thermal tolerances also varied between two widely separated populations of the intertidal mussel *M. edulis*. After five daily consecutive exposures, thermal tolerance was greater in the population from the eastern Atlantic (FR) than in the western Atlantic (USA) population, with differences of 4.5 and 2.5 °C in air and water, respectively.

For the tunicates and bryozoans, the differences in thermal tolerances paralleled differences in habitat temperatures. The populations examined along the east coast of the USA had both higher tolerances and habitat temperatures than populations along the west coast; however, east coast populations are also currently living closer to their upper tolerance limits and facing greater projected temperature increases. In contrast, differences between thermal tolerances of the two mussel populations did not correspond directly with those in habitat temperatures. Mussels from the western Atlantic had lower thermotolerance thresholds but experienced higher habitat temperatures and are residing closer to their tolerance limits. Meanwhile, mussels from the eastern Atlantic had higher thermotolerance thresholds but experienced a narrower range of habitat temperatures and may, therefore, be less vulnerable to temperature increases. It is important to note, however, that these relative climate susceptibilities could be reversed if, as shown for other marine species, the more thermotolerant populations have lower acclimation abilities (Stillman, 2003; Somero, 2010).

While the direction of the current relationship between habitat temperature and temperature tolerance differs between the subtidal epibenthic and intertidal mussel species examples, in both cases, the populations residing along the east coast of the USA (western Atlantic) appear to be most vulnerable to the projected increases in local temperatures. The highly seasonal USA east coast is characterized by a more ‘continental’ climate in relation to the more temperate ‘maritime’ climates of the USA west coast and western Europe due to differences in wind and current patterns in these regions (Seager et al., 2002). Thus, our results seem to corroborate a general difference in projected impacts between regions with ‘continental’ *versus* ‘maritime’ climates (e.g. Smith et al., 1999; Hamann and Wang, 2006), similar to the already well-appreciated differences in climate-change susceptibility across latitudes (e.g. Addo-Bediako et al., 2000; Deutsch et al., 2008; Bonebrake and Mastrandrea, 2010).

Temperature tolerances vary on both large and small spatial scales. Within the intertidal zone, average habitat temperature corresponds with tidal height, and Sokolova et al. (2000) demonstrated that temperature tolerances may be more highly variable across different tidal heights within a site than between regions. Within-region variation was demonstrated for gastropod congeners (*Littorina* sp.) from the northwest Atlantic, and, in most populations, tolerances paralleled habitat temperatures: organisms at warmer sites tended to have higher tolerances. In addition, *L. littorea* individuals from the highest latitude population examined (in northern Maine) had reduced acclimation capacities. Since high latitude locations are warming most rapidly with changing climate (Trenberth et al., 2007), northern populations may be at a greater disadvantage with continued warming.

Because geographic variation in temperature tolerance within a species could be due to acclimation and/or adaptation (Kuo and Sanford, 2009), differences in life-history strategies will likely play an important role in the response of populations to increasing temperatures (Somero, 2010). Organisms with reduced dispersal distances, limited acclimatization ability, and low thermal tolerances are considered to be at the greatest risk under a regime of climate warming (Harley et al., 2006; Deutsch et al., 2008; Somero, 2010). Conversely, organisms with pelagic larval dispersal, and therefore extensive gene flow and little genetic differentiation (Addison et al., 2008), are expected to have limited potential for local adaptation (Conover et al., 2006), and pelagic dispersal is only an advantage if gene flow is *from* more tolerant populations and *towards* less tolerant populations. Among the gastropod species examined, one has a pelagic larval stage (*L. littorea*), and this possibility for the ‘rescue’ of less tolerant, vulnerable populations exists if larvae are able to disperse from a southern, warm-adapted population with individuals of high acclimation potential to a more northern, cold-adapted population. Conversely, in the cases of *L. obtusata* and *L. saxatilis* that have direct-developing, crawl-away larvae, the exchange between populations decreases dramatically with increasing distance. Thus, the possibility of ‘rescue’ or recolonization is much less; at the same time, there may be advantages for populations of increased potential for local adaptation to current conditions (Kuo and Sanford, 2009).

Sensitivity to climate change is determined by intrinsic factors such as physiological limits, ecological traits, and genetic diversity (Williams et al., 2008). Our case studies examined geographic variation in temperature tolerance spanning a range of spatial scales and organisms, and these studies highlight several populations living closest to their upper thermal limits. In comparison to populations along the eastern Pacific or eastern Atlantic, the populations residing in the more ‘continental’ climate of the western Atlantic, including tunicates, bryozoans, and mussels, are those living nearest to their temperature tolerance thresholds. By 2099, predicted increases in temperature have the potential to seriously impact these populations, and past temperature increases since 1960 have already caused increases in mortality events and range contractions (Jones et al., 2010). In addition, sublethal physiological stress tends to reduce fitness (Menge and Sutherland, 1987), and chronic stress caused a reduction in the upper thermal tolerances of the mussel populations considered here. Thus, the increase in frequency of extreme temperatures that is predicted (see Meehl and Tebaldi, 2004) may have severe, short-term consequences for populations. Mitigation of the adverse effects of climate change will be determined by processes such as acclimatization, adaptation, and dispersal (Deutsch et al., 2008), and future studies should continue to examine whether these mechanisms are able to compensate for temperature increases.

## Acknowledgments

We especially thank R. Wong and R. Zerebecki for running many of the tolerance experiments and M. Bracken for statistical assistance and helpful comments. We thank K. Benes, N. Low, B. Taggart, D. Wethey, and S. Woodin for additional assistance and feedback. Funding was provided by a College of Biological Sciences Dean's Circle Mentorship Award from UC-Davis to CJBS and grants from NSF (OCE1039513), NOAA (NA04NOS4780264), and NASA (NNG04GE43G and NNX07AF20G). This publication is contribution number 273 of the Marine Science Center of Northeastern University. **[SS]**

## References

Addison, J.A., Ort, B.S., Mesa, K.A., Pogson, G.H., 2008. Range-wide genetic homogeneity in the California sea mussel (*Mytilus californianus*): a comparison of allozymes, nuclear DNA markers, and mitochondrial DNA sequences. Mol. Ecol. 17, 4222–4232.

Addo-Bediako, A., Chown, S.L., Gaston, K.J., 2000. Thermal tolerance, climatic variability, and latitude. Proc. R. Soc. Lond. B 267, 739–745.

Bertness, M.D., Schneider, D.E., 1976. Temperature relations of Puget Sound Thaids in reference to their intertidal distribution. Veliger 19, 47–58.

Bonebrake, T.C., Mastrandrea, M.D., 2010. Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. Proc. Natl. Acad. Sci. U. S. A. 107, 12581–12586.

Calosi, P., Bilton, D.T., Spicer, J.I., 2008. Thermal tolerance, acclimatory capacity and vulnerability to global climate change. Biol. Lett. 4, 99–102.

Chapple, J.P., Smerdon, G.R., Berry, R.J., Hawkins, A.J.S., 1998. Seasonal changes in stress-70 protein levels reflect thermal tolerance in the marine bivalve *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. 229, 53–68.

Cohen, A.N., 2005. Guide to the Exotic Species of San Francisco Bay. San Francisco Estuary Institute, Oakland, California. http://www.exoticsguide.org.

Compton, T.J., Rijkenberg, M.J.A., Drent, J., Piersma, T., 2007. Thermal tolerance ranges and climate variability: a comparison between bivalves from differing climates. J. Exp. Mar. Biol. Ecol. 352, 200–211.

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

Connell, J.H., 1972. Community interactions on marine rocky intertidal shores. Annu. Rev. Ecol. Syst. 3, 169–192.

Conover, D.O., Clarke, L.M., Munch, S.B., Wagner, G.N., 2006. Spatial and temporal scales of adaptive divergence in marine fishes and the implications for conservation. J. Fish Biol. 69, 21–47.

Davenport, J., Davenport, J.L., 2005. Effects of shore height, wave exposure and geographical distance on thermal niche width of intertidal fauna. Mar. Ecol. Prog. Ser. 292, 41–50.

Denny, M.W., Dowd, W.W., Bilir, L., Mach, K.J., 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 (this issue).

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc. Natl. Acad. Sci. U. S. A. 105, 6668–6672.

Dillon, M.E., Cahn, L.R.Y., Huey, R.B., 2007. Life history consequences of temperature transients in *Drosophila melanogaster*. J. Exp. Biol. 210, 2897–2904.

Engle, V.D., Summers, J.K., 1999. Latitudinal gradients in benthic community composition in Western Atlantic estuaries. J. Biogeogr. 26, 1007–1023.

Fangue, N.A., Hofmeister, M., Schulte, P.M., 2006. Intraspecific variation in thermal tolerance and heat shock protein gene expression in common killifish, *Fundulus heteroclitus*. J. Exp. Biol. 209, 2859–2872.

Firth, L.B., Williams, G.A., 2009. The influence of multiple environmental stressors on the limpet *Cellana toreuma* during the summer monsoon season in Hong Kong. J. Exp. Mar. Biol. Ecol. 375, 70–75.

Fitzhenry, T., Halpin, P.M., Helmuth, B., 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.

Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonne, P., Cigliano, M., Diaz, D., Harmelin, J.G., Gambi, M.C., Kersting, D.K., 2009. Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. Glob. Change Biol. 15, 1090–1103.

Gaston, K.J., Chown, S.L., 1999. Elevation and climatic tolerance: a test using dung beetles. Oikos 584–590.

Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J., Wang, G., 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integr. Comp. Biol. 46, 5–17.

Gilman, S.E., Wethey, D.S., Helmuth, B., 2006. Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. Proc. Natl. Acad. Sci. U. S. A. 103, 9560–9565.

Goto, S.G., Kimura, M.T., 1998. Heat- and cold-shock responses and temperature adaptations in subtropical and temperate species of *Drosophila*. J. Insect Physiol. 44, 1233–1239.

Grosholz, E.D., 2001. Small spatial-scale differentiation among populations of an introduced colonial invertebrate. Oecologia 129, 58–64.

Hamann, A., Wang, T., 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87, 2773–2786.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. 9, 228–241.

Helmuth, B., Mieszkowska, N., Moore, P., Hawkins, S.J., 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.

Herbert, R.J.H., Hawkins, S.J., Sheader, M., Southward, A.J., 2003. Range extension and reproduction of the barnacle *Balanus perforatus* in the eastern English Channel. J. Mar. Biol. Assoc. U. K. 83, 73–82.

Hofmann, G.E., Somero, G.N., 1995. Evidence for protein damage at environmental temperatures: seasonal changes in levels of ubiquitin conjugates and hsp70 in the intertidal mussel *Mytilus trossulus*. J. Exp. Biol. 198, 1509–1518.

Hutchins, L.W., 1947. The bases for temperature zonation in geographical distribution. Ecol. Monogr. 17, 325–335.

Intergovernmental Panel on Climate Change Working Group III, 2000. Summary for Policymakers: Emissions Scenarios. GRID-Arendal, Norway.

Janzen, D.H., 1967. Why mountain passes are higher in the tropics. Am. Nat. 101, 233–249.

Jones, S.J., Mieszkowska, N., Wethey, D.S., 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.

Jones, S.J., Lima, F.P., Wethey, D.S., 2010. Rising environmental temperatures and biogeography: poleward range contraction of the blue mussel, *Mytilus edulis* L., in the western Atlantic. J. Biogeogr. 37, 2243–2259.

Kimura, M.T., 2004. Cold and heat tolerance of drosophilid flies with reference to their latitudinal distributions. Oecologia 140, 442–449.

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

Lockwood, B.L., Somero, G.N., 2011. Invasive and native blue mussels (genus *Mytilus*) on the California coast: the role of physiology in a biological invasion. J. Exp. Mar. Biol. Ecol. this issue.

Marbà, N., Duarte, C.M., 2010. Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. Glob. Change Biol. 16, 2366–2375.

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

Meehl, G.A., Covey, C., Delworth, T.L., Latif, M., Mcavaney, B., Mitchell, J.F.B., Stouffer, R.J., Taylor, K.E., 2007. The WCRP CMIP3 multimodel dataset. Bull. Am. Meteorol. Soc. 88, 1383–1394.

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

Mieszkowska, N., Leaper, R., Moore, P., Kendall, M.A., Burrows, M.T., Lear, D., Poloczanska, E., Hiscock, K., Moschella, P.S., Thompson, R.C., Herbert, R.J., Laffoley, D., Baxter, J., Southward, A.J., Hawkins, S.J., 2005. Marine biodiversity and climate change: assessing and predicting the influence of climatic change using intertidal rocky shore biota. Final Report for United Kingdom Funders: Mar. Biol. Assoc. Occas. Publ., 20, pp. 1–53.

Miller, L.P. 2008. Life on the edge: morphological and behavioral adaptations for survival on wave-swept shores. Ph.D. Thesis, Stanford University, 205 pp.

Miller, L.P., Harley, C.D.G., Denny, M.W., 2009. The role of temperature and desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia gigantea*. Funct. Ecol. 23, 756–767.

Newell, R.C., 1969. Effect of fluctuations in temperature on the metabolism of intertidal invertebrates. Am. Zool. 9, 293–307.

Newell, R.C., 1979. Biology of Intertidal Animals. Marine Ecological Surveys Ltd., Faversham. 781 pp.

O'Neill, G.A., Hamann, A., Wang, T., 2008. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. J. Appl. Ecol. 45, 1040–1049.

Pearce, J.B., 1969. Thermal addition and the benthos, Cape Cod Canal. Chesapeake Sci. 10, 227–233.

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

Poloczanska, E.S., Smith, S., Faunonneta, L., Healy, J., Tibbetts, I.R., Burrows, M.T., Richardson, A.J., 2011. Little change in the distribution of rocky shore faunal communities on the Australian east coast after 50 years of rapid warming. J. Exp. Mar. Biol. Ecol. 400, 145–154 (this issue).

R Core Development Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rajagopal, S., Van Der Velde, G., Van Der Gaag, M., Jenner, H.A., 2005. Factors influencing the upper temperature tolerances of three mussel species in a brackish water canal: size, season, and laboratory protocols. Biofouling 21, 87–97.

Read, K.R.H., Cumming, K.B., 1967. Thermal tolerance of the bivalve mollusks *Modiolus modiolus* (L.), *Mytilus edulis* (L.) and *Brachidontes demissus* Dillwyn. J. Comp. Biochem. Physiol. 22, 149–155.

Reid, D.G., 1996. Systematics and Evolution of *Littorina*. Dorset Press, Dorchester, Dorset, UK.

Reynolds, R.W., Smith, T.M., Liu, C., Chelton, D.B., Casey, K.S., Schlax, M.G., 2007. Daily high-resolution-blended analyses for sea surface temperature. J. Clim. 20, 5473–5496.

Ritchie, J., 1927. Report on the prevention of the growth of mussels in submarine shafts and tunnels at Westbank Electricity Station, Portobello. Trans. R. Scot. Soc. Arts 19, 1–20.

Seager, R., Battisti, D.S., Yin, J., Gordon, N., Naik, N., Clement, A.C., Cane, M.A., 2002. Is the Gulf Stream responsible for Europe's mild winters? Q. J. R. Meteorol. Soc. 127, 2563–2586.

Smith, R.C., Ainley, D., Baker, K., Domack, E., Emslie, S., Fraser, B., Kennett, J., Leventer, A., Mosley-Thompson, E., Stammerjohn, S., Vernet, M., 1999. Marine ecosystem sensitivity to climate change. Bioscience 49, 393–404.

Sokolova, I.M., Granovitch, A.I., Berger, V.J., Johannesson, K., 2000. Intraspecific physiology variability of the gastropod *Littorina saxatilis* related to the vertical shore gradient in the White and North Seas. Mar. Biol. 137, 297–308.

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

Somero, G.N., 2005. Linking biogeography to physiology: evolutionary and acclimatory adjustments of thermal limits. Front. Zool. 2, 1–9.

Somero, G.N., 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine the 'winners' and 'losers'. J. Exp. Biol. 213, 912–920.

Sorte, C.J.B., Hofmann, G.E., 2005. Thermotolerance and heat-shock protein expression in Northeastern Pacific *Nucella* species with different biogeographical ranges. Mar. Biol. 146, 985–993.

Sorte, C.J.B., Stachowicz, J.J., in review. Patterns and processes of compositional change in a California epibenthic community. Mar. Ecol. Prog. Ser.

Sorte, C.J.B., Williams, S.L., Carlton, J.T., 2010a. Marine range shifts and species introductions: comparative spread rates and community impacts. Glob. Ecol. Biogeogr. 19, 303–316.

Sorte, C.J.B., Williams, S.L., Zerebecki, R.A., 2010b. Ocean warming increases threat of invasive species in a marine community. Ecology 91, 2198–2204.

Sorte, C.J.B., Fuller, A., Bracken, M.E.S., 2010c. Impacts of a simulated heat wave on composition of a marine community. Oikos 119, 1909–1918.

Southward, A.J., Hawkins, S.J., Burrows, M.T., 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. J. Therm. Biol. 20, 127–155.

Stenseng, E., Braby, C.E., Somero, G.N., 2005. Evolutionary and acclimation-induced variation in the thermal limits of heart function in congeneric marine snails (genus *Tegula*): implications for vertical zonation. Biol. Bull. 208, 138–144.

Stillman, J.H., 2002. Causes and consequences of thermal tolerance limits in rocky intertidal porcelain crabs, genus *Petrolisthes*. Integr. Comp. Biol. 42, 790–796.

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

Stillman, J.H., Somero, G.N., 2000. A comparative analysis of the upper thermal tolerance limits of eastern Pacific porcelain crabs, genus *Petrolisthes*: influences of latitude, vertical zonation, acclimation, and phylogeny. Physiol. Biochem. Zool. 73, 200–208.

Tomanek, L., Somero, G.N., 1999. Evolutionary and acclimation-induced variation in the heat-shock responses of congeneric marine snails (genus *Tegula*) from different thermal habitats: implications for limits of thermotolerance and biogeography. J. Exp. Biol. 202, 2925–2936.

Trenberth, K.E., Jones, P.D., Ambenje, P., Bojariu, R., Easterling, D., Klein Tank, A., Parker, D., Rahimzadeh, F., Renwick, J.A., Rusticucci, M., Soden, B., Zhai, P., 2007. Observations: surface and atmospheric climate change. Climate change 2007: the physical science basis. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 235–236.

Urban, H.J., 1994. Upper temperature tolerance of ten bivalve species off Peru and Chile related to *El Niño*. Mar. Ecol. Prog. Ser. 107, 139–145.

Vellend, M., Harmon, L.J., Lockwood, J.L., Mayfield, M.M., Hughes, A.R., Wares, J.P., Sax, D.F., 2007. Effects of exotic species on evolutionary diversification. Trends Ecol. Evol. 22, 481–488.

Vernberg, F.J., Vernberg, W.B., 1967. Thermal limits of southern hemisphere *Uca* crabs. Oikos 18, 118–123.

Wethey, D.S., 2002. Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. Integr. Comp. Biol. 42, 872–880.

Wethey, D.S., Woodin, S.A., 2008. Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. Hydrobiologia 606, 139–151.

Wethey, D.S., Woodin, S.A., Hilbish, T.J., Jones, S.J., Lima, F.P., Brannock, P.M., 2011. Response of intertidal populations to climate: effects of extreme events *versus* long term change. J. Exp. Mar. Biol. Ecol. this volume.

Widmer, A.M., Carveth, C.J., Bonar, S.A., Simms, J.R., 2006. Upper temperature tolerance of loach minnow under acute, chronic, and fluctuating thermal regimes. Trans. Am. Fish. Soc. 135, 755–762.

Williams, G.A., De Pirro, M., Leung, K.M.Y., Morritt, D., 2005. Physiological responses to heat stress on a tropical shore: the benefits of mushrooming behaviour in the limpet *Cellana grata*. Mar. Ecol. Prog. Ser. 292, 213–224.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., Langham, G., 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biol. 6, 2621–2626.

Wolcott, T.G., 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at "limiting factors". Biol. Bull. 145, 389–422.

Yund, P.O., Stires, A., 2002. Spatial variation in population dynamics in a colonial ascidian (*Botryllus schlosseri*). Mar. Biol. 141, 955–963.

Zerebecki, R.A., Sorte, C.J.B., in press. Temperature tolerance and stress proteins as mechanisms of invasive species success. PLoS One.

Zippay, M.L., Hofmann, G.E., 2010. Physiological tolerances across latitudes: thermal sensitivity of larval marine snails (*Nucella* spp.). Mar. Biol. 157, 707–714.