

April 2011

Geographic Variation in Temperature Tolerance as an Indicator of Potential Population Responses to Climate Change

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Recommended Citation

Cascade J.B. Sorte, Sierra J. Jones, and Luke P. Miller. "Geographic Variation in Temperature Tolerance as an Indicator of Potential Population Responses to Climate Change" *Journal of Experimental Marine Biology and Ecology* (2011): 209-217.

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1 **Geographic variation in temperature tolerance as an indicator of potential population**
2 **responses to climate change**

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24 Keywords: Acclimatization, Biogeography, Climate change, Ecological forecasting,

25 Ecophysiology, Temperature tolerance

26

27 Abstract

28 The temperature tolerances of individuals in geographically separated populations of a
29 single species can be used as indicators of each population's potential to persist or become
30 extinct in response to climate change. We evaluated the population-level variation in temperature
31 tolerance in populations of several marine invertebrate taxa, including bryozoans, tunicates,
32 bivalves, and gastropods, separated by distances of <200 km to >5,000 km. We then combined
33 physiological thermotolerance data with current temperature data and climate change predictions
34 to predict which of these populations may be most vulnerable to future changes. In a trans-
35 continental comparison of four subtidal epibenthic species, we show that populations on the east
36 coast of the United States, which experienced higher habitat temperatures than those on the west
37 coast, had higher thermal tolerances but lived closer to individuals' tolerance limits. Similarly,
38 temperature tolerances varied between western and eastern Atlantic populations of the mussel
39 *Mytilus edulis*; however, these differences only emerged after repeated exposures to high
40 temperatures. Furthermore, the less thermotolerant *M. edulis* population in the western Atlantic
41 was more susceptible to temperature increases, as evidenced by a recent range contraction. Thus,
42 for both the subtidal epibenthic and intertidal mussel species, we identified the western Atlantic
43 as a 'hot spot' of populations susceptible to climate change compared to those in the eastern
44 Pacific and eastern Atlantic, respectively. Finally, because current tolerances are not the sole
45 indicators of individuals' abilities to cope with temperature increases, we also assessed the
46 possibility for acclimatization to facilitate the persistence of populations *via* the buffering of
47 temperature effects. We show that, for four populations of intertidal *Littorina* snail species in the
48 northwest Atlantic, most populations were able to overcome geographic differences in
49 temperature tolerance *via* acclimation. When acclimation capacity is low, the potential for

50 “rescue” may depend on the particular species’ life-history strategy and dispersal ability. For
51 example, although individuals from the coldest-adapted population of *Littorina littorea* were
52 unable to acclimate as quickly as those from more southern populations, this species has a
53 pelagic larval stage and, thus, the greatest dispersal potential of these littorines. Together, these
54 studies highlight the importance of considering variation in temperature tolerance between
55 populations within species to improve the forecasting of changes in the abundances and
56 distributions of species in response to climate warming.

57

58 **1. Introduction**

59 As mean and extreme temperatures increase in marine systems, the likelihood that a
60 given population persists is partly related to the physiological capacity of organisms to tolerate
61 elevated temperatures (Hutchins, 1947; Newell, 1969; 1979). Temperature clearly affects
62 species’ distribution patterns: a strong relationship between upper temperature tolerance and
63 maximum habitat temperature has been demonstrated for many species (Wolcott, 1973;
64 Tomanek and Somero, 1999; Stillman and Somero, 2000; Stillman, 2002; Wethey, 2002; Miller
65 et al., 2009; Lockwood & Somero, 2011, this volume). Shifts in species’ ranges have been linked
66 to rising mean temperatures (Southward et al., 1995; Herbert et al., 2003; Mieszkowska et al.,
67 2005; Helmuth et al., 2006; Wethey and Woodin, 2008; Sorte et al., 2010a; Poloczanska et al.,
68 2011, this volume). Furthermore, increases in extreme temperatures have been followed by
69 mortality events (Garrabou et al., 2009; Firth and Williams, 2009; Jones et al., 2009, 2010;
70 Marbà and Duarte, 2010). Recent studies have focused on interspecific differences in
71 temperature tolerance – particularly between closely-related congeners – to identify organismal
72 and ecological characteristics of the “winners” and “losers” of climate change (Somero, 2010). It

73 has been suggested that species with higher temperature tolerances will be better able to cope
74 with global warming (Calosi et al., 2008) or, conversely, that more warm-adapted species will be
75 at a disadvantage because they tend to live closer to their absolute tolerance limits (Stillman and
76 Somero, 2000; Somero, 2005, 2010; Compton et al., 2007; Bonebrake and Mastandrea, 2010)
77 and have lower acclimation potentials (Stillman, 2003; Somero, 2005; Stenseng et al., 2005;
78 Ghalambor et al., 2006). In this paper, we treat these hypotheses by taking a more intimate look
79 at geographic variation in temperature tolerance *within* species, including its potential as an
80 indicator of regions likely to experience local extinction or population persistence.

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

95 Here, we consider geographic variation in the upper limit of temperature tolerance in the
96 context of predicting population-level responses to climate change. Populations likely to persist
97 in the warmer conditions predicted with climate change are those in which, as diagrammed in
98 Fig. 1: (i) individuals have high temperature tolerances, (ii) individuals have the capacity, *via*
99 phenotypic plasticity, to acclimate to higher temperatures, or (iii) populations of tolerant
100 individuals – those that either already have high tolerance or have high acclimatization capacity
101 – can disperse and re-seed areas of less tolerant populations (Deutsch et al., 2008). Thus,
102 populations that are more prone to local extinction will be those in which individuals have low
103 temperature tolerance, low acclimatization capacity, and/or low dispersal ability (Deutsch et al.,
104 2008). We present three case studies in which we combine physiological thermotolerance data
105 with current temperature data and climate change predictions. By examining ecophysiological
106 and biogeographic patterns for a diverse set of marine taxa – including bryozoans, tunicates,
107 bivalves, and gastropods – we provide a starting point for addressing broad questions about
108 climate-change impacts relevant to many systems, both marine and terrestrial, such as:

109 (1) How do temperature tolerances vary geographically over small (i.e. regional) and large (i.e.
110 trans-continental and trans-oceanic) scales?

111 (2) Are populations with higher average temperature tolerances likely to be at an advantage due
112 to their capability of surviving at increased temperatures or at a disadvantage due to a narrower
113 distance between their tolerance limits and projected temperature exposures?

114 (3) Do more tolerant populations possess the acclimation capacity and dispersal potential that
115 could “rescue” vulnerable populations from local extinction?

116

117 **2. Epibenthic fouling species: a trans-continental comparison**

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

124 2.1. Methods

125 In July and August 2010, four epibenthic species settled naturally onto plastic tiles
126 (Duplos; LEGO Group, Billund, Denmark) deployed in marinas at approx. 1 m depth. The
127 tunicates *Botrylloides violaceus* and *Botryllus schlosseri* were collected on tiles deployed at
128 Lynn, Massachusetts (42.4577°N, 70.9434°W), and the tunicate *Diplosoma listerianum* and
129 bryozoan *Bugula neritina* were similarly obtained at Hawthorne Cove Marina in Salem,
130 Massachusetts (42.5195°N, 70.8872°W). West coast individuals were collected at Bodega
131 Harbor, California (38.3311°N, 123.0567°W) in July and August 2009.
132 Lethal temperatures were determined following the methods detailed in Sorte et al. (2010b, for
133 the west coast individuals) with exceptions as noted below. Briefly, individuals were acclimated
134 in the laboratory in running seawater at ambient temperature (approx. 17°C) for 24 h, after which
135 tiles containing 2 individuals (colonies) of a single species were placed in separate 1 L
136 experimental chambers (note: one individual per chamber was used for *B. neritina* when
137 necessary due to low recruitment). Temperature was raised at a rate of 1°C per 5 min until the
138 treatment temperature was reached, and mortality was assessed following a 24 h temperature
139 exposure (at approx. 21, 25, 29, and 34°C; actual chamber temperatures were used in the
140 analyses). LT_{50} values were calculated by Probit analysis in SAS v 9.1 (SAS Institute, Cary,

141 North Carolina, USA) and were compared to values for west coast populations determined in
142 July and August 2009 (Zerebecki and Sorte, in review).

143 Projected temperature changes for the east and west coast sites studied were calculated
144 from nine global circulation models available as part of the World Climate Research
145 Programme's Coupled Model Intercomparison Project 3 (CMIP3; Meehl et al., 2007). We
146 calculated changes in average monthly sea surface temperatures using the Intergovernmental
147 Panel on Climate Change SRES A1B emissions scenario (IPCC Working Group III, 2000). Data
148 from each climate model were processed in the program R v 2.11.1 (R Core Development Team,
149 2010) to extract the projected average monthly temperatures for the ocean grid cell closest to
150 each of our sites. We used temperature estimates from 1961-90 as a baseline for comparison
151 against the future projections for 2090-99. We calculated the mean temperature in each time
152 period (1961-90 and 2090-99) separately for each month (January - December) and used the
153 difference between the two time periods as our estimate of future temperature change for each
154 month of the year. The average temperature change for the entire year was calculated from the
155 monthly changes.

156 2.2. Results & Discussion

157 Lethal temperatures were higher for east coast than west coast populations of all four
158 epibenthic species (1-sample t-test: $t = 6.1207$, $df = 3$, $p = 0.0088$; Fig. 2). The difference
159 between LT_{50} values for east and west coast populations ranged from 1.1°C for *B. schlosseri* to
160 2.1°C for *B. violaceus*. Absolute LT_{50} values (east/west coast) were $29.4 / 28.3^{\circ}\text{C}$ for *B.*
161 *schlosseri*, $27.4 / 25.3^{\circ}\text{C}$ for *B. violaceus*, $29.1 / 27.9^{\circ}\text{C}$ for *D. listerianum*, and $26.4 / 24.4^{\circ}\text{C}$ for
162 *B. neritina*. The magnitude of variation in temperature tolerance between east and west coast
163 populations was strongly related to the LT_{50} : species that were *less* thermotolerant on the west

164 coast displayed a *greater difference* in LT_{50} between the east and west coasts ($F_{1,2} = 25.92$, $p =$
165 0.0365 ; $R^2 = 0.93$).

166 Temperature tolerances also paralleled habitat temperatures. Mean summertime water
167 temperature in Massachusetts was 2.4°C warmer than in California (June - August, 2006-2010),
168 and annual temperature range was twice as broad – 24.9 vs. 12.4°C – in the eastern USA (Fig. 3;
169 Sorte and Stachowicz, in review; MA data from NOAA National Buoy Data Center
170 <www.nbdc.noaa.gov> Boston Harbor station BHB3M). The east coast populations are currently
171 living closer to individuals' summer tolerance limits: maximum summertime temperatures were
172 4.4°C higher in Massachusetts, and these local temperature maxima were within 3.9°C of
173 populations' LT_{50} values on the east coast but 6.7°C greater than those on the west coast. The
174 species living closest to its tolerance limit, the bryozoan *Bugula neritina*, encountered maximum
175 temperatures within 2.2°C and 4.6°C of its LT_{50} on the east and west coast, respectively.

176 If acclimatization and adaptation abilities do not vary between populations, then the east
177 coast populations will continue to be more susceptible due to expected increases in ocean
178 temperatures. When projected temperature increases are taken into account, summer (June –
179 August) sea surface temperatures on the east coast are likely to approach or exceed the LT_{50}
180 values of the two species living closest to their tolerance limits, *Bugula neritina* and *Botrylloides*
181 *violaceus*, by the end of the 21st century. In Massachusetts, mean summer and annual sea surface
182 temperatures are projected to rise by 3.0 and 3.3°C , respectively. In California, mean increases of
183 2.4 and 2.7°C are predicted for summer and annual sea surface temperatures, respectively, which
184 are still below the four species' LT_{50} values. However, for California populations of *B. neritina*
185 and *B. violaceus*, this increase in summer temperatures could nevertheless elicit 20-30%
186 mortality (Fig. 2).

187 These data support, at the population level, the documented pattern that species living at
188 higher temperatures occur closer to their absolute tolerance limits (i.e. Stillman and Somero,
189 2000; Somero, 2005, 2010; Compton et al., 2007; Deutsch et al., 2008), and they suggest that
190 east coast populations will be at a disadvantage in warmer conditions relative to west coast
191 populations. This prediction, however, neglects these species' potentials for acclimatization and
192 local adaptation, which may, if representative of genotypic variation, be indicated by two studies
193 showing significant phenotypic variation over small distances. For example, Grosholz (2001)
194 showed local adaptation in minimum temperature tolerance of *Botrylloides* sp. between sites
195 separated by <60 km, and variation in habitat temperatures may have caused differences in
196 *Botryllus schlosseri* population dynamics between sites only <20 km distant (Yund and Stires,
197 2002). Such fine-scale population adaptation is possible for species that lack a pelagic larval
198 stage and recruit extremely locally, such as the intertidal dogwhelk *Nucella canaliculata* (Kuo
199 and Sanford, 2009) and the four epibenthic species treated here. Clearly, these epibenthic species
200 have the potential for acclimatization and/or rapid local adaptation: all four are non-natives that
201 were most, if not all, introduced to California during the past century (Cohen, 2005), and already
202 there are apparent differences in temperature tolerance between east and west coast populations.
203 Interestingly, the two least tolerant species also showed the greatest individual variation in
204 temperature tolerance (as indicated by the shallower slope of their tolerance curves in Fig. 2)
205 suggesting – if phenotypic variation indicates genotypic variation – that populations of these
206 species have a greater potential for adaptation.

207 A comparison with previous research in the Bodega Harbor epibenthic community
208 showed strong effects of age on survival rate and that the impacts of increased temperatures can
209 be exacerbated – and even reversed – in older individuals. For example, a 3-day experimental

210 heat wave of 24.5°C caused 100% mortality in adults of the three tunicate species considered
211 here but little to no mortality in adults of the bryozoan *Bugula neritina* (Sorte et al., 2010c),
212 which is the most susceptible of these species as a juvenile. Furthermore, on the west coast, LT₅₀
213 values were lower for native species than for non-native species overall (Sorte et al., 2010b).
214 Thus, both on the east and west coasts, different life stages, and the respective suite of native
215 species, may be living more ‘on the edge’ in epibenthic communities.

216

217 **3. Marine mussels: a cross-ocean comparison**

218 Compared to the shallow subtidal systems discussed above, where temperatures vary by
219 <25°C annually and less on shorter (i.e. daily) timescales, the marine intertidal zone is a
220 physically rigorous habitat in which rapid and extreme fluctuations in temperature occur on a
221 daily basis. Mussels in the genus *Mytilus* are major space occupiers of marine intertidal habitats,
222 and, like tunicates and bryozoans, are sedentary. Because their responses to environmental
223 change are largely unmitigated by behavior, their upper intertidal and equatorward geographic
224 distributions are often constrained by physiological limits, such as thermal tolerance.

225 *3.1. Methods*

226 The upper thermal tolerance of the mussel *Mytilus edulis* was determined for western and
227 eastern Atlantic populations using the methods presented in Jones et al. (2009). Adult mussels
228 were collected from Nahant, Massachusetts, USA (42.4195°N, 70.9023°W) on 20 June 2006 and
229 from Luc-sur-Mer, Normandy, France (49.3110°N, 0.3555°W) on 5 July 2010. Shell lengths
230 (mean ± SD) were 45.2 ± 5.0 mm and 27.14 ± 2.15 mm for the mussels from the USA and
231 France (FR), respectively. Upon collection, animals were transported in coolers to temperature-
232 controlled recirculating seawater tanks (“control” tanks: Living Streams; Frigid Units, Toledo,

233 Ohio, USA) with a semidiurnal tidal cycle at the University of South Carolina (Columbia, South
234 Carolina, USA) and acclimated for one week.

235 Water temperature in the control tanks was maintained at approximate ambient field
236 temperatures of 18°C (USA) and 19°C (FR) for the duration of the experiment. Most thermal
237 tolerance experiments previously conducted on *M. edulis* examined the response to water
238 temperatures alone (Ritchie, 1927; Read and Cumming, 1967; Pearce, 1969; Rajagopal et al.,
239 2005). However, because these intertidal mussels are exposed to both submerged and aerial
240 conditions, each experimental trial was run in both water and air at a range of environmentally
241 realistic temperatures, including 25, 30, 32.5, 35, and 40°C, with three replicates of 5 animals for
242 each temperature treatment ($n = 15$ per temperature x medium treatment). Reach-in incubators
243 were maintained for the duration of the experiment at each of the target temperatures to within \pm
244 0.25°C. Aquaria (38 L) were placed inside the incubators, and in this manner both the air and
245 water treatments could be run simultaneously. The role of evaporative cooling in mussels (i.e.
246 gaping) was assumed to be negligible, as Fitzhenry et al. (2004) showed that mussel body
247 temperatures were not related to gaping ability.

248 Mussels were exposed to the same temperature for a 6 h period each day, simulating one
249 tidal event per day, and the experiment was run for 5 consecutive days as a means of discerning
250 the effects of thermal history. Following each exposure event, mussels were removed from the
251 incubators and returned to the respective control tanks (with tidal period) for a recovery period of
252 18 h, after which we counted the numbers of dead individuals. The recovery period simulated
253 natural conditions in which a period of stress is followed by an extended period of immersion
254 and/or a second emersion during the morning or night when air temperatures are relatively low.
255 Mussels from the air and water treatments were held in separate control tanks on opposing tidal

256 cycles in order to ensure proper cycling of emersion and immersion periods. The LT_{50} values
257 were calculated for each exposure event by linear interpolation of the graphs of cumulative
258 survival *versus* temperature in R v 2.8.1 (R Core Development Team, 2010)

259 3.2. Results & Discussion

260 Multiple exposures decreased temperature tolerances for both the USA and French
261 populations of *M. edulis* (Fig. 4). For both populations, there was a fast initial decline in
262 tolerance, and tolerance tended to plateau after the third exposure. The two populations tended to
263 diverge after the second exposure, and population differences in LT_{50} continued to increase
264 through the fifth exposure. By the fifth exposure, mussels from the French population of *M.*
265 *edulis* had thermal tolerances that exceeded those from the USA population by 4.5°C and 2.5°C
266 in air and water, respectively. Thus, there was a common relationship between LT_{50} and number
267 of exposures for both populations, with thermal tolerance decreasing as a function of increasing
268 exposures. These findings indicate the importance of accounting for thermal history when
269 examining survival within an ecological context.

270 When LT_{50} values were averaged across the 5 exposures, tolerances were higher for FR
271 than USA mussels in both air (Welch Two-Sample t-test; $t = -2.776$, $df = 5.109$, $p = 0.038$) and
272 water (Welch Two-Sample t-test; $t = -1.966$, $df = 7.846$, $p = 0.086$). However, in this cross-ocean
273 comparison of *M. edulis*, differences in temperature tolerances did not parallel those in habitat
274 temperatures. Daily optimally interpolated sea surface temperature (OISST) data on a 0.25° grid
275 (Reynolds et al., 2007) were obtained for the nearest pixel corresponding with collection sites for
276 the period January 1998-December 2008. There was little to no difference between USA and FR
277 locations in annual maximum ocean temperatures, which ranged from 19.6-22.7°C in FR, with
278 an average maximum of 20.8°C, and between 19.3-21.3°C in the USA, with an average

279 maximum of 20.7°C. Considering that an immersed mussel will have the same body temperature
280 as the water (Gilman et al., 2006), the differences in immersed thermal tolerances between the
281 two populations are surprising since maximum habitat water temperatures are similar.

282 Interestingly, the seasonal range in temperatures experienced was, on average, 4.3°C greater in
283 the USA/western Atlantic where the population is composed of less thermally tolerant
284 individuals.

285 The disconnection between habitat temperatures and thermal tolerances was even more
286 pronounced for air temperatures. Hourly air temperature data were obtained from the National
287 Climatic Data Center (www.ncdc.noaa.gov) for Boston, Massachusetts, USA (42.3584°N,
288 71.0598°W; Site ID: 725090) and Cap de la Hève, France (49.5167°N, 0.0667°E; Site ID:
289 070280) for the period January 1998 - December 2009. Annual average maximum temperature
290 for FR ranged between 29.4-36.1°C, with an average maximum of 31.2°C, while the range for
291 the USA was 33.3-37.8°C, with an average maximum of 35.2°C. As with sea surface
292 temperatures, the seasonal range in air temperature was much greater for the western Atlantic
293 population: 50.8°C in the USA *versus* 35.6°C in the eastern Atlantic. The disparity between
294 tolerance and habitat temperatures could partially reflect the fact that while emerged at low tide,
295 the body temperature of a mussel may be higher than the ambient air temperature (Hofmann and
296 Somero, 1995; Denny et al., 2011, this volume). However, overall, the suggestion that more
297 warm-adapted species tend to live closer to their thermal tolerance limits (Stillman and Somero,
298 2000; Somero, 2005, 2010; Compton et al., 2007; Bonebrake and Mastandrea, 2010) does not
299 appear to be the case for these mussel populations. The population with the highest thermal
300 tolerances (FR) experienced cooler temperatures and a narrower seasonal temperature range

301 whereas mussels in the population with lower thermal tolerances (USA) inhabited locations with
302 higher maximum habitat temperatures and a broader temperature range.

303 Repeated, chronic exposures to high temperatures have been demonstrated to have
304 negative effects on a variety of organisms, impacting foraging behavior in the marine intertidal
305 seastar *Pisaster ochraceus* (Pincebourde et al., 2008), growth of the benthic stream minnow
306 *Rhinichthys cobitis* (Widmer et al., 2006), and fecundity and viability in the fruit fly *Drosophila*
307 *melanogaster* (Dillon et al., 2007). A decrease in upper thermal tolerance after repeated
308 exposures has been observed in other mussel species, including *Mytilus trossulus*, *M.*
309 *galloprovincialis*, and *M. californianus*, from the west coast of the USA (S. Jones and N.
310 Mieszkowska, unpubl. data), in addition to that shown here for *M. edulis* from the Atlantic.
311 While the physiological mechanisms underlying these results are unknown, we suggest that they
312 could reflect costs associated with sublethal stress, such as the expression of heat-shock proteins.
313 Hilbish et al. (unpubl. data) determined that the threshold induction temperature of the heat-
314 shock response for *M. edulis* from the USA was between 29 and 32°C, which is very close to the
315 LT₅₀ values derived from the temperature tolerance experiments. Repeated exposures to such
316 high temperatures may override the heat-shock response: Chapple et al. (1998) found that *M.*
317 *edulis* could not acclimate to temperatures above 28.5C, and Hilbish et al. (unpubl. data) showed
318 that heat-shock protein expression increased with temperatures up to 32°C but declined
319 dramatically at 35°C. These data indicate that the heat-shock response may not be able to
320 compensate for repeated exposures to high temperatures, increasing the probability of mortality
321 with more frequent heat exposure.

322 Many intertidal organisms tend to live at the limits of their temperature tolerances, both
323 within the intertidal zone and on a geographic scale (Connell, 1961, 1972; Wolcott, 1973;

324 Newell, 1979; Wethey, 2002; Jones et al., 2009), and *Mytilus* is no exception. Analysis of
325 intertidal temperature records for the east coast of the USA and northern Europe indicated that
326 between two and five consecutive daily exposures to high temperatures typically occur during a
327 spring tidal cycle (S. Jones, unpubl. data; B. Helmuth and N. Mieszkowska, unpubl. data). As a
328 result, high mortality in response to these repeated exposures has been documented (Jones et al.,
329 2010). Increases in ambient temperature due to climatic change, and increases in the frequency
330 of heat waves, could therefore affect both small- and large-scale distributions. For *M. edulis*
331 along the western Atlantic, a range contraction of approximately 350 km in response to rising
332 temperatures has already been documented (Jones et al., 2010). However, such a change in
333 distribution has not been seen for *M. edulis* along the eastern Atlantic (Wethey et al., 2011, this
334 volume), which could be due to the fact that temperature tolerances in northern France are much
335 higher than those on the USA east coast.

336

337 **4. Within-region variation in northwest Atlantic littorine snails**

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

344 *4.1. Methods*

345 Individuals of three *Littorina* species – *L. littorea*, *L. obtusata*, and *L. saxatilis* – were
346 collected between 19 July and 11 August 2010 from four locations in the northeastern USA:

347 northern Maine (Hamilton Cove, near Quoddy Head; 44.7867°N, 67.0064°W), southern Maine
348 (Pemaquid Point; 43.8406°N 69.5098°W), Massachusetts (East Point, Nahant; 42.4195°N,
349 70.9023°W), and Rhode Island (Kings Beach; 41.3856°N, 71.6639°W; except no *L. saxatilis*
350 were collected from this site). Individuals were kept in the laboratory with running seawater at
351 17°C for acclimation periods of either 5 days or 3 weeks with $n = 12$ per species x site x
352 acclimation time. Snails acclimated for 3 weeks were fed *ad libitum* with the alga *Fucus*
353 *vesiculosus*, replaced twice per week.

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

368 *4.2. Results & Discussion*

369 Temperature tolerance varied geographically between field-acclimatized (5-day
370 acclimated) populations of *L. obtusata* (site $F_{3,44} = 9.08$, $p < 0.0001$) and *L. saxatilis* (site $F_{2,32} =$
371 4.66 , $p = 0.017$). For the low to mid-intertidal littorines, *L. littorea* and *L. obtusata*, temperature
372 tolerance of field-acclimatized individuals was highest in the Rhode Island population (i.e. the
373 warmest site) and lowest in the Maine populations (Fig. 5). *L. littorea* tolerances tended to
374 increase monotonically with decreasing latitude (site $p = 0.103$) whereas *L. obtusata* tolerances
375 were lowest in the southern Maine population ($p < 0.0001$). Interestingly, for the high intertidal
376 species *L. saxatilis*, tolerance was highest at the northern Maine location ($p = 0.017$), although,
377 since this species was not collected at the warmest Rhode Island site, our latitudinal comparison
378 was more limited. Thus, these *Littorina* species tend to have less tolerant phenotypes north of
379 Cape Cod, a biogeographic barrier between different thermal habitats (Engle and Summers,
380 1999; Fig. 5A). At the same time, our comparisons indicate that differences between sites
381 separated by <200 km (e.g. *L. obtusata* in southern versus northern Maine) can be as significant
382 as, or greater than, those between sites with >500 km geographic separation. Similarly,
383 Davenport and Davenport (2005) showed that within a suite of 10 rocky intertidal species,
384 differences in thermal niche widths were often the same or greater between sites within a single
385 region than between multiple regions (but see Fanguie et al., 2006 for an example of a species
386 with tolerance variation only between, but not within, regions).

387 Temperature tolerances tended to increase after 3 weeks of laboratory acclimation for all
388 11 populations examined (Fig. 5A). However, the effect of the acclimation period on the degree
389 of geographic variation in temperature tolerance between populations differed by species. For *L.*
390 *obtusata* and *L. saxatilis*, the significant geographic variation in tolerance disappeared (*L.*
391 *obtusata*: site $p > 0.2$) or was obscured (*L. saxatilis*: site $p = 0.062$) after the acclimation period.

392 Conversely, for *L. littorea*, the geographic variation became more pronounced after acclimation
393 (site $F_{3,40} = 4.09$, $p = 0.0127$), with the acclimation capacity of the northern Maine snails lagging
394 behind that of the more southern populations. Among these 11 populations of littorine snails,
395 only two populations – *L. littorea* from northern Maine and *L. saxatilis* from southern Maine –
396 were unable to ‘keep up with’ their southern counterparts that were more tolerant and better able
397 to acclimate (Fig. 5). Of these species, *L. littorea*, which releases eggs that hatch into pelagic
398 larvae, has a greater ability for more tolerant populations to recolonize and ‘rescue’ less tolerant
399 populations than the other two direct-developing species that have shorter dispersal distances
400 (Reid, 1996).

401 Among these three littorines, *L. obtusata*, while able to acclimate to increased
402 temperature, had tolerance levels that were still well below those of the other species. Average
403 tolerance scores for *L. obtusata* were 1.2 ± 0.2 for both Maine populations after the acclimation
404 period, or slightly higher than ‘moribund’ (score of 1) which Bertness and Schneider (1976)
405 suggested is approximately the point of 50% mortality. Even if some populations manage to
406 acclimatize sufficiently to avoid high mortality (e.g. the Rhode Island population achieved a
407 tolerance score of 1.6 ± 0.2 after the 3 week acclimation), dispersal distance is low due to this
408 species’ life-history strategy. However, *L. obtusata* are also often found amongst the blades of
409 their furoid algal food source (C. Sorte, unpubl. data) which could provide a temperature refuge.
410 Thus, for littorines as well as other marine species, microhabitat buffering (i.e. movement into
411 nearby algal canopies, rock crevices, and cracks) and other behavioral responses (e.g., Williams
412 et al., 2005; Miller, 2008) could ameliorate stressful exposures (Williams et al., 2008). Overall,
413 this case study illustrates the need to consider acclimatization capacity when attempting to

414 project population- and species-level responses to climate change, and future studies exploring
415 the role of dispersal ability and behavioral responses are warranted.

416

417 **5. Overview**

418 The geographic distribution of a species tends to be closely linked with climate, and
419 understanding that relationship is imperative when predicting impacts of climatic change.

420 Hutchins (1947) argued that geographic limits are set by thermal tolerances, and in many cases
421 correspondences have been demonstrated between geographic and physiological limits (e.g.

422 Vernberg and Vernberg, 1967; Sorte and Hofmann, 2005; Jones et al., 2009; Somero, 2010).

423 Marine ectotherms, such as tunicates, bryozoans, bivalves, and gastropods, may be particularly
424 sensitive indicators of climate change (Somero, 2002; Mieszkowska et al., 2005; Helmuth et al.,
425 2006). While studies of species-specific temperature tolerance are relatively common, fewer data
426 are available regarding how tolerances vary on a geographic scale between populations within a
427 single species (O'Neill et al., 2008; Kuo and Sanford, 2009; but see e.g. Urban, 1994; Zippay
428 and Hofmann, 2010).

429 We examined the variation in thermal tolerances between widely geographically
430 separated populations within species of tunicates (*Diplosoma listerianum*, *Botrylloides violaceus*,
431 and *Botryllus schlosseri*), bryozoans (*Bugula neritina*), and bivalves (*Mytilus edulis*). Contrary to
432 some previous findings (e.g. Goto and Kimura, 1998; Gaston and Chown, 1999; Addo-Bediako
433 et al., 2000; Kimura, 2004), our results indicate that upper thermal thresholds do vary between
434 geographically separated populations. Among the subtidal tunicates and bryozoans, differences
435 in LT₅₀ values ranged from 1.1 to 2.1°C between the west and east coast USA populations, and,
436 in each case, tolerance was significantly greater for populations on the east coast. Upper thermal

437 tolerances also varied between two widely separated populations of the intertidal mussel *M.*
438 *edulis*. After five daily consecutive exposures, thermal tolerance was greater in the population
439 from the eastern Atlantic (FR) than in the western Atlantic (USA) population, with differences of
440 4.5 and 2.5°C in air and water, respectively.

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

454 While the direction of the current relationship between habitat temperature and
455 temperature tolerance differs between the subtidal epibenthic and intertidal mussel species
456 examples, in both cases, the populations residing along the east coast of the USA (western
457 Atlantic) appear to be most vulnerable to the projected increases in local temperatures. The
458 highly seasonal USA east coast is characterized by a more ‘continental’ climate in relation to the
459 more temperate ‘maritime’ climates of the USA west coast and western Europe due to

460 differences in wind and current patterns in these regions (Seager et al., 2002). Thus, our results
461 seem to corroborate a general difference in projected impacts between regions with ‘continental’
462 *versus* ‘maritime’ climates (e.g. Smith et al., 1999; Hamann and Wang, 2006), similar to the
463 already well-appreciated differences in climate-change susceptibility across latitudes (e.g. Addo-
464 Bediako et al., 2000; Deutsch et al., 2008; Bonebrake and Mastandrea, 2010).

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

475 Because geographic variation in temperature tolerance within a species could be due to
476 acclimation and/or adaptation (Kuo and Sanford, 2009), differences in life-history strategies will
477 likely play an important role in the response of populations to increasing temperatures (Somero,
478 2010). Organisms with reduced dispersal distances, limited acclimatization ability, and low
479 thermal tolerances are considered to be at the greatest risk under a regime of climate warming
480 (Harley et al., 2006; Deutsch et al., 2008; Somero, 2010). Conversely, organisms with pelagic
481 larval dispersal, and therefore extensive gene flow and little genetic differentiation (Addison et
482 al., 2008), are expected to have limited potential for local adaptation (Conover et al., 2006), and

483 pelagic dispersal is only an advantage if gene flow is *from* more tolerant populations and *towards*
484 less tolerant populations. Among the gastropod species examined, one has a pelagic larval stage
485 (*L. littorea*), and this possibility for the ‘rescue’ of less tolerant, vulnerable populations exists if
486 larvae are able to disperse from a southern, warm-adapted population with individuals of high
487 acclimation potential to a more northern, cold-adapted population. Conversely, in the cases of *L.*
488 *obtusata* and *L. saxatilis* that have direct-developing, crawl-away larvae, exchange between
489 populations decreases dramatically with increasing distance. Thus, the possibility of ‘rescue’ or
490 recolonization is much less; at the same time, there may be advantages for populations of
491 increased potential for local adaptation to current conditions (Kuo and Sanford, 2009).

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

506 determined by processes such as acclimatization, adaptation, and dispersal (Deutsch et al., 2008),
507 and future studies should continue to examine whether these mechanisms are able to compensate
508 for temperature increases.

509

510 **Acknowledgments**

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

518

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- 744

745 **Figure Legends**

746

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

754

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

762

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

765

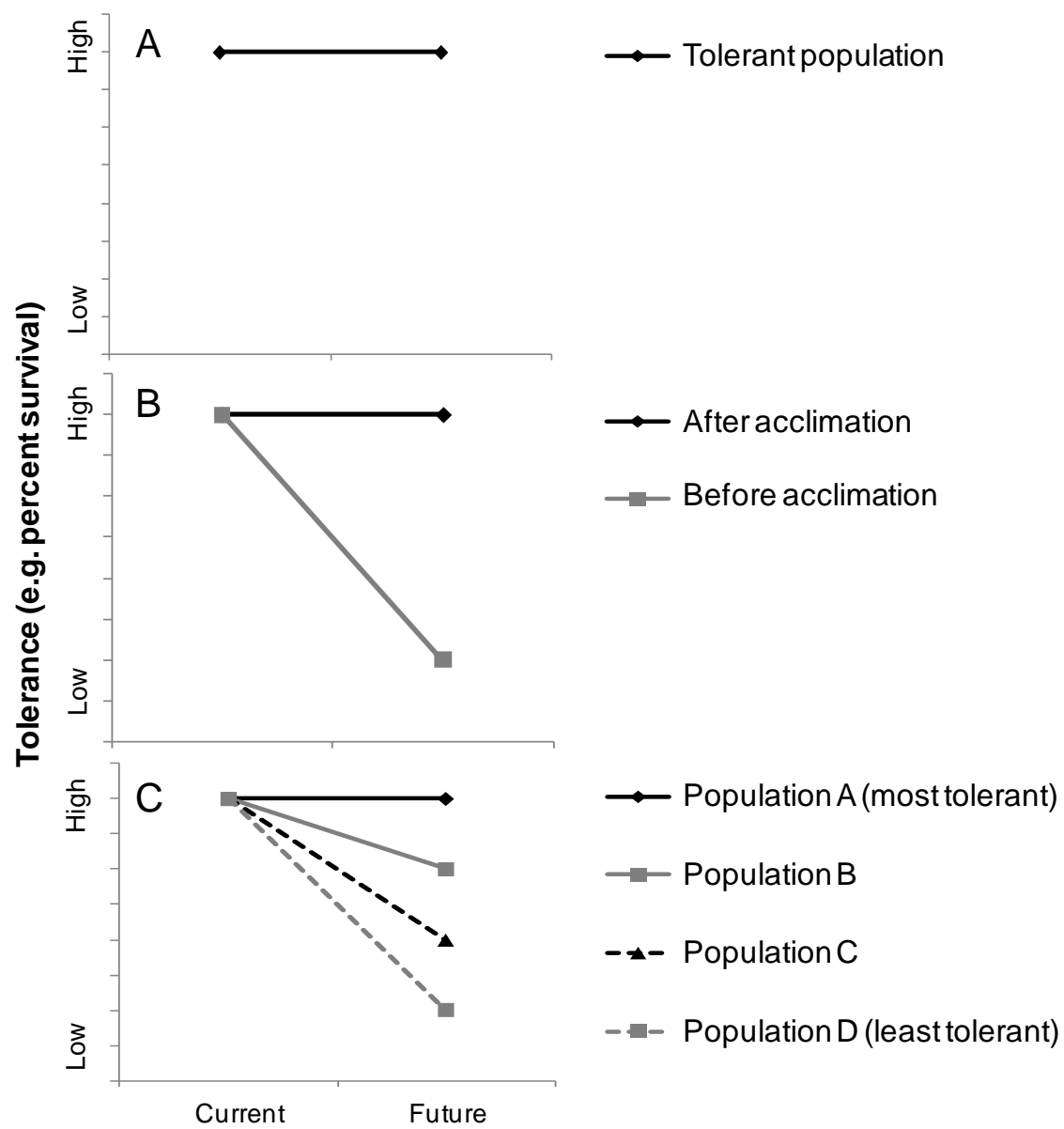
766 **Figure 4.** Calculated LT_{50} values (± 1 SE) for *Mytilus edulis* after five consecutive exposure
767 events in (A) air and (B) water. Mussels were collected from Normandy, France (dotted line,
768 closed circles) and Massachusetts, USA (solid line, open circles).

769

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

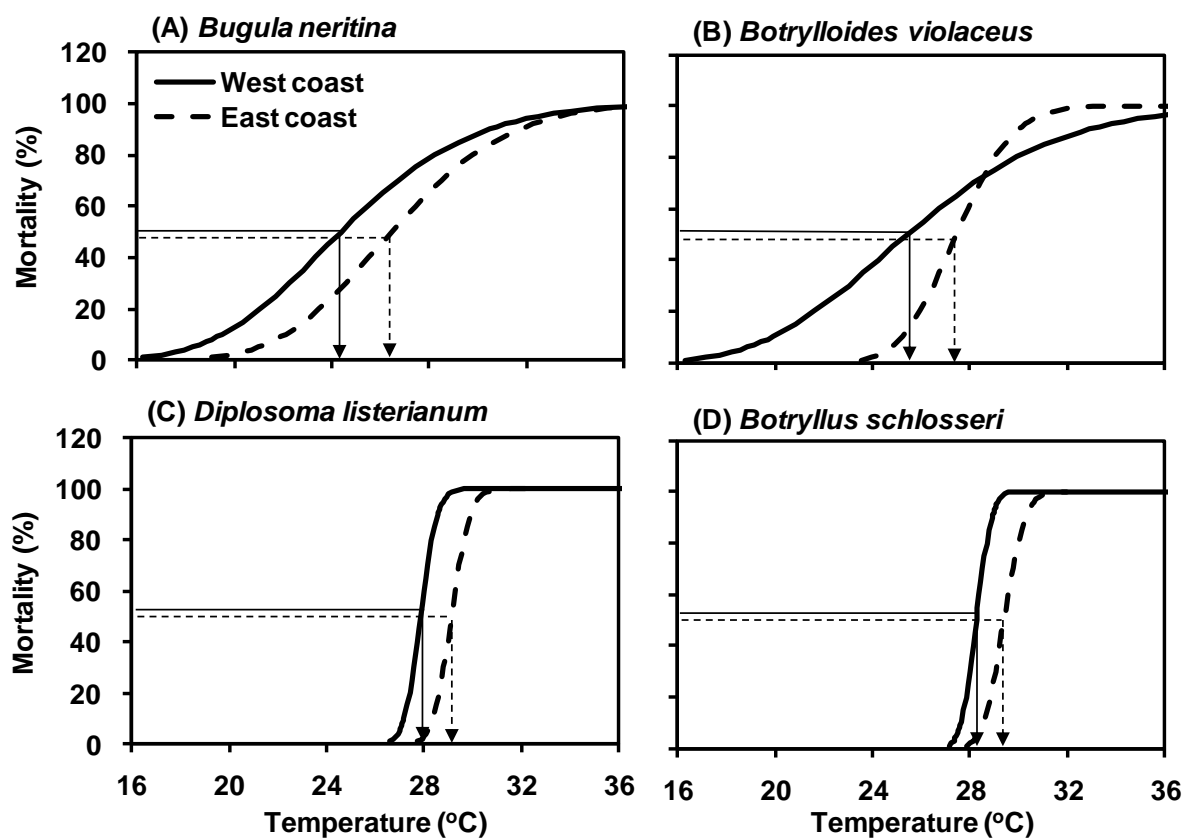
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782 **Figure 1.**

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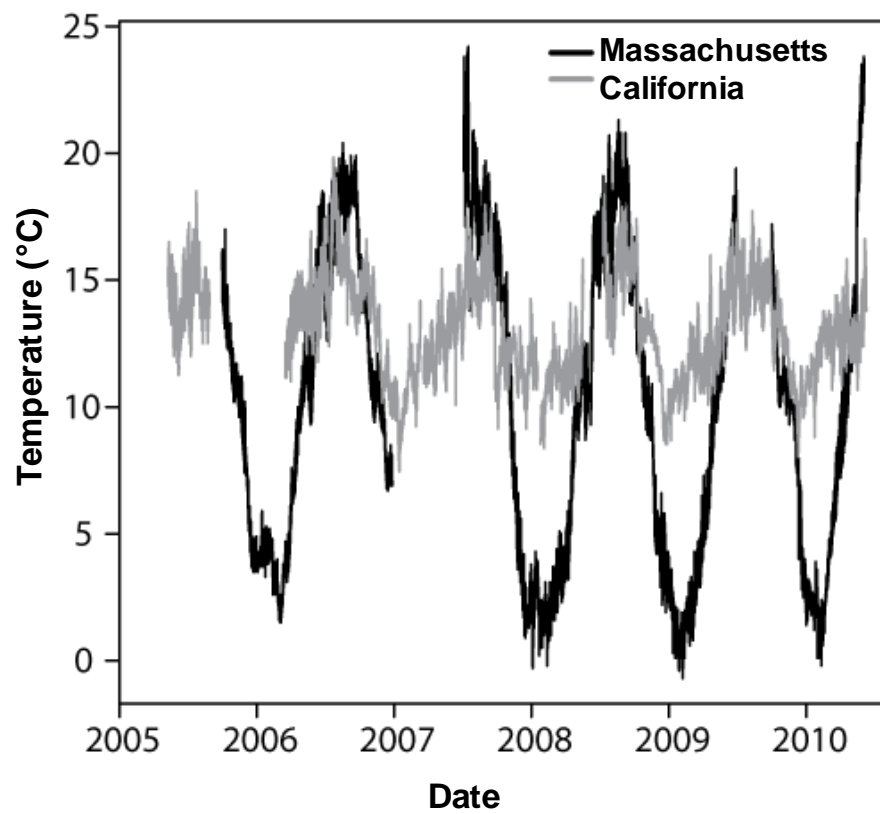
785 **Figure 2.**

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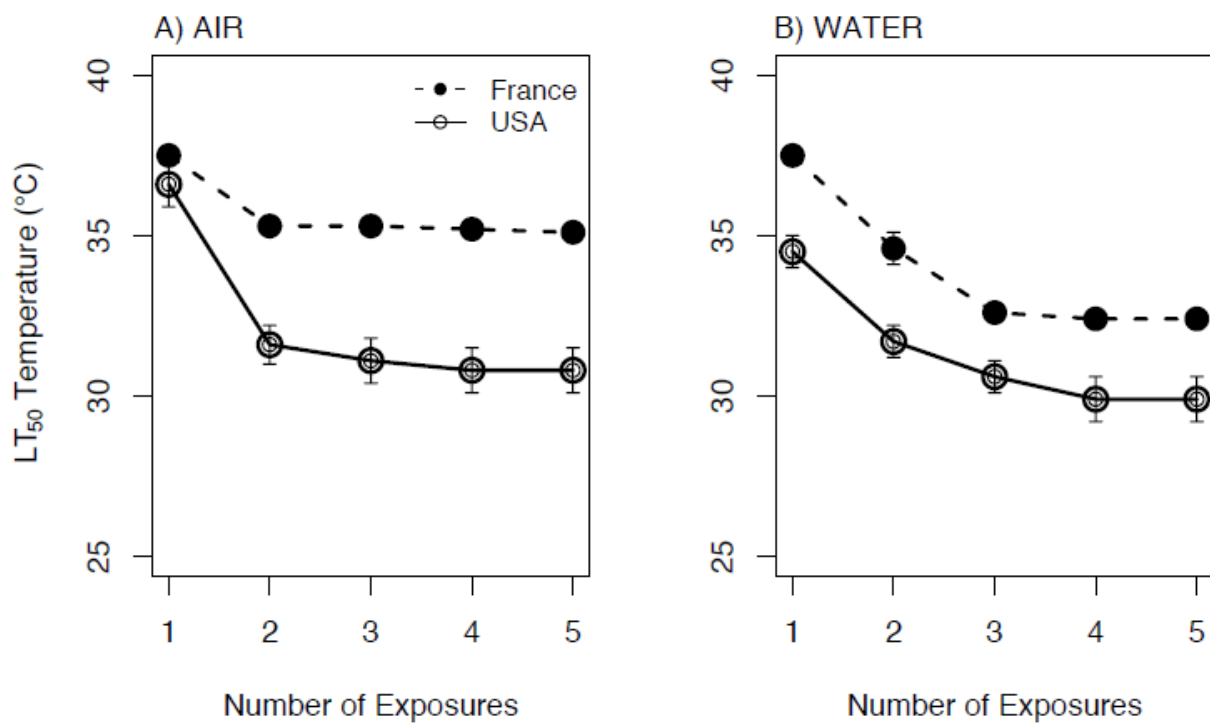
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790 **Figure 3.**

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793 **Figure 4.**

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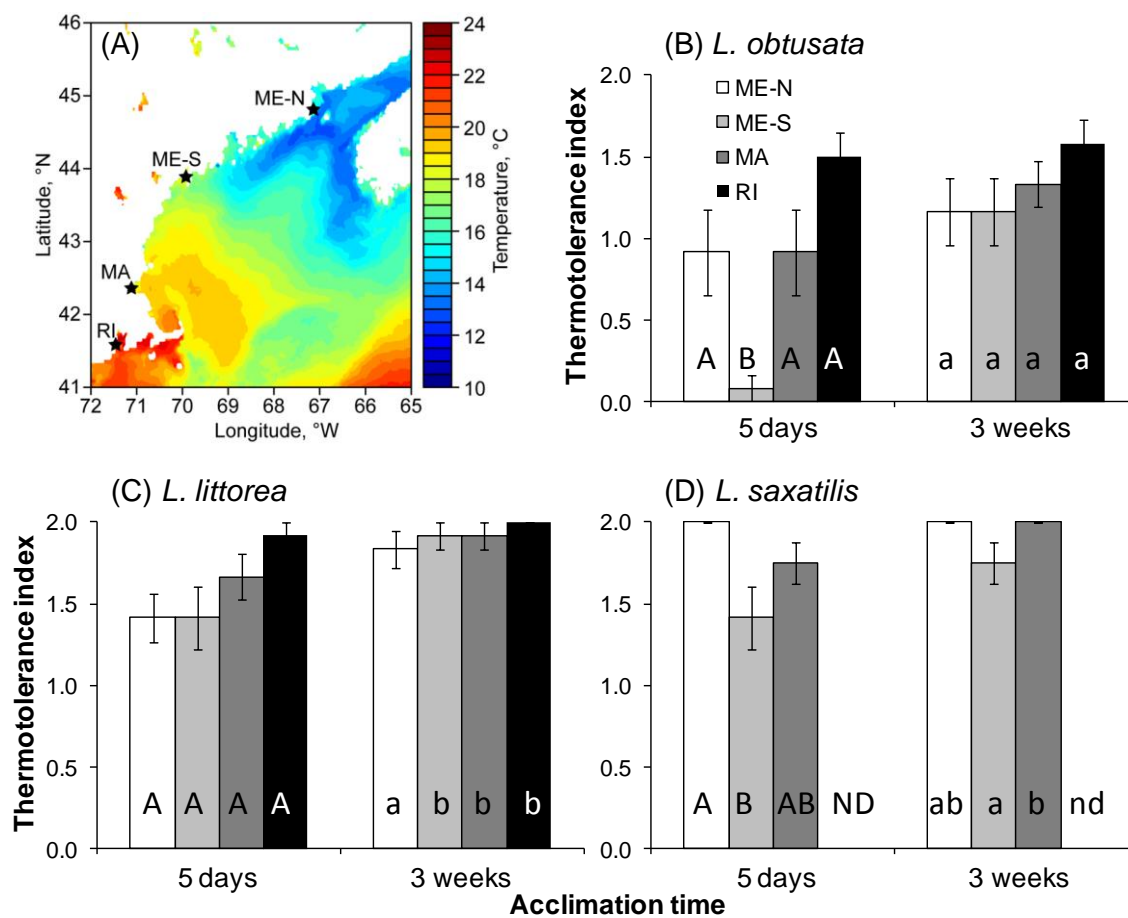
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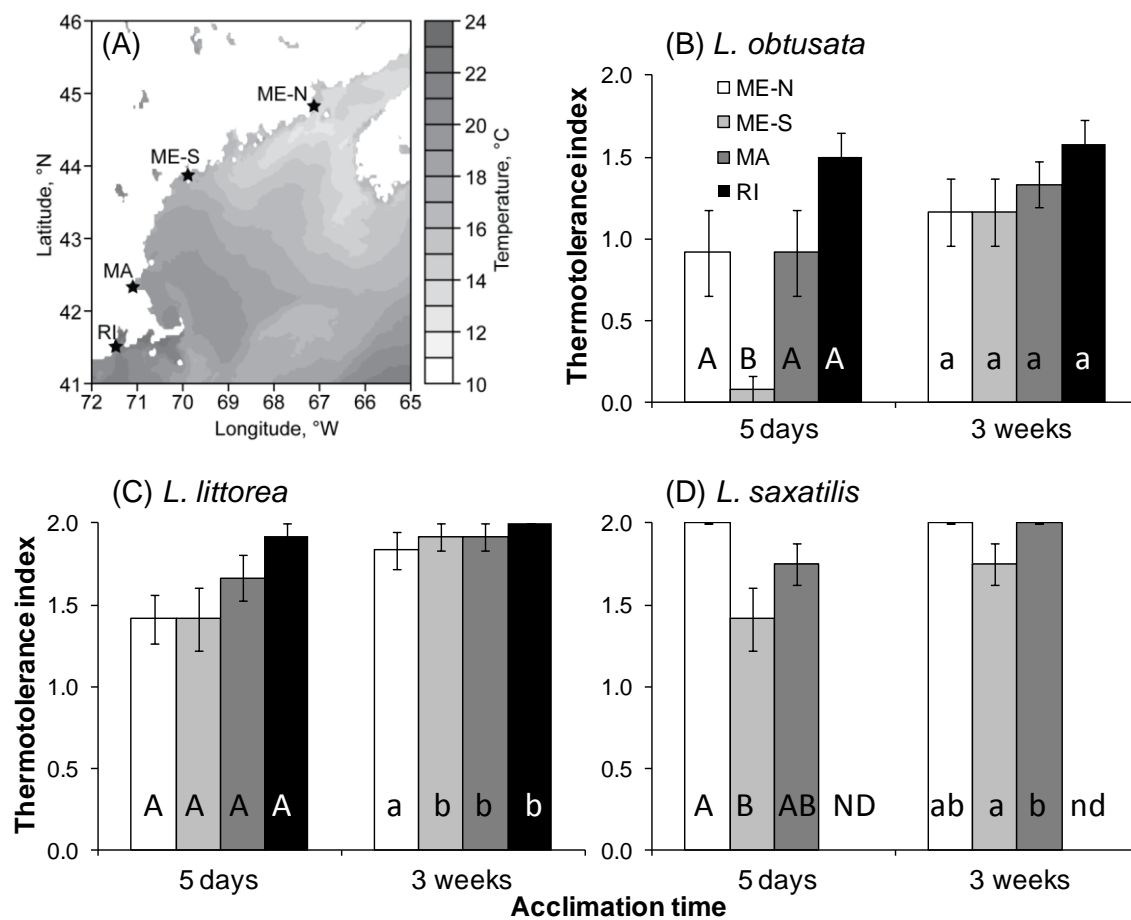
807 **Figure 5 (color, for online version).**



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811 **Figure 5 (grayscale, for print version).**

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