

Predicting the sensitivity of marine populations to rising temperatures

A Randall Hughes^{1*}, Torrance C Hanley¹, Althea FP Moore¹, Christine Ramsay-Newton², Robyn A Zerebecki¹, and Erik E Sotka³

Oceans are warming at rates faster than marine species have experienced over the previous 400,000 years. Our quantitative review across a wide range of marine taxa revealed that increases in temperature that occur above mean annual temperature (MAT) generally lower population survival and reproduction. Furthermore, these effects are likely to be increasingly detrimental, particularly for survival, as the magnitude of warming increases. Although we found evidence for considerable variation within and between populations in response to increasing temperatures, whether this existing variation will allow for evolutionary rescue is uncertain. Importantly, a simple metric (ie MAT) facilitates evaluation of the effects of increasing temperatures on the survivorship and reproduction of most populations, even those for which limited data on thermal sensitivity are available. This approach improves our understanding of population-level responses to climate change, which is critical for adaptation planning that aims to sustain and restore vulnerable populations.

Front Ecol Environ 2019; 17(1): 17–24, doi:10.1002/fee.1986

Both land and ocean temperatures are changing rapidly as a result of human activities that have substantially increased atmospheric concentrations of carbon dioxide and other greenhouse gases (Diffenbaugh and Field 2013; Laffoley and Baxter 2016). Predicting and managing the effects of global climate change require knowledge of population vulnerability (ie the propensity or predisposition to be adversely affected; IPCC 2014). While scientific literature lacks consensus regarding the definition of species vulnerability (Pacifi *et al.* 2015), researchers suggest that it is a function of both intrinsic and extrinsic factors and includes exposure, sensitivity, and adaptive capacity (Williams *et al.* 2008; Foden *et al.* 2013). Exposure is defined as the extent of climate change likely to be experienced by a species or place and depends on the rate and magnitude of climate change (temperature, precipitation, sea-level rise, etc) in habitats and regions occupied by the species (Williams *et al.* 2008). Sensitivity is the degree to which a system or species is affected by changes in climate (IPCC 2014) and can be determined by traits that are intrinsic to a species (Foden *et al.* 2013). Adaptive capacity is defined as the ability of systems, institutions, humans, and other organisms to adjust to potential damage, to take advantage of opportunities, or to respond to consequences (IPCC 2014). For species or populations, such capacity may be enhanced through natural selection and other evolutionary mechanisms, and it depends on both intrinsic factors (phenotypic plasticity, genetic diversity, evolutionary rates, dispersal and colonization ability) and extrinsic factors (rate, magnitude, and nature of climatic change) (Dawson *et al.* 2011).

Changes in temperature can alter species distributions and phenology, species interactions, community diversity, and ecosystem function (Parmesan and Yohe 2003; Vasseur *et al.* 2014). Increases in temperature generally benefit population fitness until temperatures exceed a thermal optimum (T_{opt} ; Kingsolver and Huey 2008), after which population fitness often declines (Figure 1; Huey *et al.* 2012). Population thermal performance curves (TPCs) have facilitated climate adaptation planning and management by providing critical data for identifying species that are vulnerable to rising temperatures (Vasseur *et al.* 2014).

Although experimental assessments of thermal sensitivity in survivorship, growth, and reproduction have a long history in both terrestrial (Huey and Kingsolver 1989) and marine (Kinne 1960) populations, these studies have only rarely included a sufficient range of temperature treatments to fully describe both the rise and fall of the fitness response. This has precluded their use in syntheses of species vulnerability requiring TPCs that capture species' entire thermal response (eg Deutsch *et al.* 2008; Araújo *et al.* 2013). In order to evaluate the sensitivity of diverse and less studied taxa to warming, researchers need simple methods that would facilitate use of all existing information on population responses to temperature change (Williams *et al.* 2008; Huey *et al.* 2012; Nadeau *et al.* 2017). In the absence of full TPCs, potential proxies could include maximum critical temperature (the temperature above T_{opt} at which mortality occurs), mean body temperature in the field, and preferred body temperature in the lab (Huey *et al.* 2012). However, these require meticulous experimental manipulations, and data therefore remain unavailable for most taxa and populations (but see Comte and Olden [2017] for an analysis of freshwater and marine ray-finned fishes).

In this study, we examined the ability of mean annual temperature (MAT) to predict the sensitivity of taxonomically

¹Department of Marine and Environmental Science, Northeastern University, Nahant, MA *(rhughes@northeastern.edu); ²Department of Life Sciences, Mitchell College, New London, CT; ³Department of Biology and Grice Marine Laboratory, College of Charleston, Charleston, SC

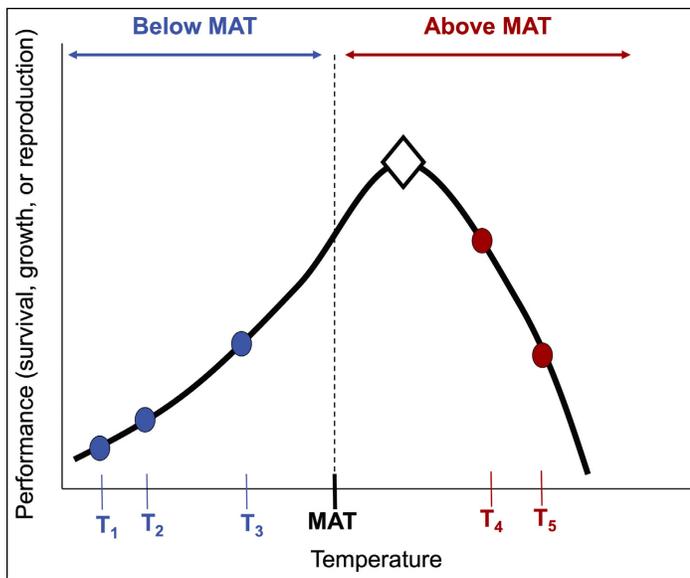


Figure 1. Hypothetical thermal performance curve (TPC) for a single population. The open diamond represents the thermal optimum (T_{opt}); MAT represents mean annual water temperature for this population, which is below T_{opt} ; closed circles symbolize experimental temperatures tested, with the color indicating whether the temperature is below MAT (blue) or above MAT (red). The positive sloping section of the curve to the left of T_{opt} can be referred to as the “rise”, whereas the negative sloping section to the right is the “fall”. In this hypothetical example, T_1 would be the control temperature for calculations of sensitivity (S) below MAT, whereas T_4 would be the control temperature for calculations of S above MAT; T_2 , T_3 , and T_5 are simply other hypothetical experimental temperatures.

diverse marine populations to temperature change. MAT is an easily measured and readily available indicator of the thermal environment, and can be used to predict the thermal optima of animals that depend on external sources of body heat (ie ectotherms) in aquatic ecosystems (Portner *et al.* 2014), though not in semi-terrestrial and fully terrestrial systems (Huey *et al.* 2012). This contrast may result in part because terrestrial body temperatures are influenced by convection, radiation, conduction, and evaporation (Huey *et al.* 2012), and the latter three of these heat-transfer mechanisms are relatively weak under water. While a relationship between MAT and T_{opt} would facilitate predictions of whether local warming trends will increase or decrease population fitness (ie the “rise” and “fall” components of Figure 1), T_{opt} data are not always available. We therefore propose that MAT could serve to evaluate climate change sensitivity of aquatic ectotherms when fully characterized TPCs or T_{opt} are unavailable.

We created a database of experiments that measured at least one fitness metric (survival, growth, and/or reproduction; WebTable 1; WebPanel 1) in response to at least two temperature treatments for at least two marine populations in a laboratory environment (ie “common garden” studies). We estimated MAT for the source location of each population in the database and tested whether it predicted the direction and magnitude of sensitivity in fitness metrics for those same populations, which represent a range of taxonomic groups (algae,

plants, invertebrates, and vertebrates; Figure 2). It should be noted that our focus here is on predicting population sensitivity and not adaptive capacity to respond to temperature changes. We hypothesized that if MAT approximates T_{opt} , then temperature increases below MAT would increase fitness (positive sensitivity), whereas temperature increases above MAT would decrease fitness (negative sensitivity) (Figure 1; Huey *et al.* 2012). We then focused on the “above MAT” category to examine the ability of a suite of intrinsic and extrinsic factors to predict the magnitude and direction of sensitivity to rising temperatures. These factors and their hypothesized relationships with thermal sensitivity are summarized in Table 1. Our analysis suggested that MAT is an informative first-order approximation of population thermal optima in fitness that could be used to evaluate and manage marine populations faced with warming seas.

■ Methods

We focused our meta-analysis on studies examining at least two populations of a species to test for population-level variation in thermal responses. We conducted an exhaustive search of studies published before January 2016 in Google Scholar and Web of Science (ISI) using the keywords “marine OR estuar*” AND “common garden OR laboratory” AND “growth OR survival OR reproduction OR fecundity” AND “temperature”. We also targeted reviews and meta-analyses on related topics, checking both the literature cited in each paper and the studies subsequently citing each paper. Field studies, including reciprocal transplant designs, were excluded from our analysis, in part because results of this methodology have been reviewed and analyzed previously (Wu *et al.* 2011). The database included marine populations from four broad taxonomic groups (algae, plants, invertebrates, and vertebrates) distributed across tropical and temperate regions around the world (WebPanel 1). Because we were interested in individual-level fitness responses, we restricted our search to studies measuring individual growth and reproduction and excluded studies measuring only population growth of microbial, fungal, and microalgal populations (see Thomas *et al.* [2016] and references therein for an analysis of thermal adaptation in marine phytoplankton). Our final database included 46 studies (see WebPanel 1 for a list of studies, and WebPanel 2 for sample sizes for each analysis).

We calculated mean annual temperature (MAT) and seasonality (ie standard deviation of mean monthly temperatures; Deutsch *et al.* 2008) for each population by extracting daily water temperatures from 2014 within a $1^\circ \times 1^\circ$ latitude area around the source location of each population from a high-resolution ($0.25^\circ \times 0.25^\circ$) dataset (Banzon *et al.* 2014). Data were extracted using NetCDF in the R package “ncdf” (Pierce 2015; <http://cirrus.ucsd.edu/~pierce/ncdf>). We used the MAT associated with the source location of each population to categorize paired temperature treatments as “below MAT” (ie control and treatment temperatures lower than population MAT; fitness



Figure 2. Representative species from each of the taxonomic groups included in our analysis: (a) Atlantic cod (*Gadus morhua*, vertebrates); (b) Arctic sea moss (*Acrosiphonia arcta*, algae); (c) Baltic isopod (*Idotea balthica*, invertebrates); and (d) black mangrove (*Avicennia germinans*, plants).

responses to increased temperature expected to be positive) or “above MAT” (ie control and treatment temperatures higher than population MAT; fitness responses to increased temperature expected to be negative) (Figure 1; Huey *et al.* 2012).

We then calculated the magnitude and direction of thermal sensitivity using the effect size metric S (Wu *et al.* 2011):

$$S = (E - C) / (T_E - T_C), \quad (\text{Eq. 1})$$

where E and C are the mean responses of the experimental treatment and control groups, respectively, and T_E and T_C are the temperatures in the experimental treatment and control groups, respectively. Unlike other standard effect size metrics (eg log response ratio), S normalizes the absolute response relative to the magnitude of the temperature difference between the treatment and control. For consistency, the lowest temperature treatment was assigned as the control for “below MAT” comparisons, and the lowest temperature treatment above MAT was assigned as the control for “above MAT” comparisons. Therefore, a positive S indicates a positive response to increased temperature and a negative S indicates a negative response to increased temperature.

For each study, we also recorded extrinsic and intrinsic factors that would potentially affect responses to temperature change. Intrinsic factors included in our analyses were taxonomic group (alga, plant, invertebrate, or vertebrate), study species, population, and life-history stage (juvenile versus adult, with studies spanning multiple life-history stages being classified according to their life-history stage at the end of the

experiment). Extrinsic factors included population-specific latitude, seasonality of water temperature (sensu Deutsch *et al.* 2008), and the difference between an experimental treatment temperature and the mean annual water temperature (TRT–MAT) for each temperature tested. We also recorded the fitness response metric (survival, growth, or reproduction), the fitness response variable (eg proportion survival, growth rate), and sample size for each treatment combination. Because rate metrics (eg growth rate) may respond differently to temperature than non-rate metrics (eg final biomass) (Forster *et al.* 2011), we categorized fitness response variables accordingly and analyzed them separately. When we focused on a subset of the database to analyze survival, growth, or reproduction responses separately for each taxonomic group, there were only sufficient data to analyze either rates or non-rates: survival, reproduction, and plant growth response variables were non-rate metrics, whereas algal, invertebrate, and vertebrate growth responses were rate metrics (WebTable 1). If a study reported multiple measures of survival, growth, or reproduction (eg change in length and change in weight), we included all relevant response metrics in our analysis and ran a randomization test to determine whether the results changed depending on the particular metrics included (see WebPanel 2 for details). For studies reporting survival at multiple time points, we included data from the first and last time points as measures of shortest- and longest-term survivorship. For studies that did not report latitude and longitude, we estimated population location based on information provided in the text.

Table 1. Hypotheses regarding the relationships between thermal sensitivity and the intrinsic and extrinsic factors examined in this study

Factor	Expected relationship with thermal sensitivity	Representative reference(s)
<i>Intrinsic</i>		
Taxonomic group	Taxonomic groups differ in patterns of sensitivity	Araújo <i>et al.</i> (2013)
Species	Species differ in patterns of sensitivity	Huey and Stevenson (1979); Deutsch <i>et al.</i> (2008); Araújo <i>et al.</i> (2013)
Population	Populations do not all respond similarly to changing temperature	Davis <i>et al.</i> (2005); Angert <i>et al.</i> (2011); Gaitan-Espitia <i>et al.</i> (2014)
Life-history stage	Developmental stages have different sensitivities	Boyd <i>et al.</i> (2016); Sinclair <i>et al.</i> (2016)
<i>Extrinsic</i>		
Seasonality	Magnitude of temperature variation is positively related to thermal tolerance	Deutsch <i>et al.</i> (2008); Sheldon and Tewksbury (2014); Stuart-Smith <i>et al.</i> (2017)
Latitude	Tropical species are more vulnerable to increases in mean temperature	Deutsch <i>et al.</i> (2008)
	Mid-latitude species are more vulnerable to increases in temperature	Kingsolver <i>et al.</i> (2013); Vasseur <i>et al.</i> (2014)
Experimental temperature relative to MAT	Relative temperature change is more important than absolute temperature change for fitness	Deutsch <i>et al.</i> (2008)

For each fitness metric, we used a linear fixed-effects model to test the ability of taxonomic group, MAT (categorical variable: experimental temperatures above or below MAT), and their interactions to predict thermal sensitivity. We included a fixed effect of population nested within species and within study, with studies weighted by sample size. To examine the effects of temperature increases above MAT on thermal sensitivity, we used a linear fixed-effects model with independent effects of population seasonality, population latitude, TRT–MAT, life-history stage, and population. On the basis of documented relationships from past studies (eg Deutsch *et al.* 2008; Sunday *et al.* 2014), we tested both linear and quadratic functions for seasonality, latitude, and TRT–MAT. We lacked power to adequately assess interactions among factors. Some of our predictor variables were significantly correlated with one another (eg latitude and seasonality; WebFigure 1), but the strength of these relationships was always $R^2 < 0.06$, so we retained each factor in our analysis. All analyses were conducted in R (v3.1.2; R Core Team 2018).

Results

Population MAT and taxonomic group were significant predictors of sensitivity in all metrics of fitness, including survival (taxa×MAT $F_{6,431} = 37.77$, $P < 0.0001$; Figure 3a), reproduction (taxa×MAT $F_{6,181} = 3.68$, $P = 0.003$; Figure 3b), and growth (taxa×MAT $F_{6,509} = 7.19$, $P < 0.0001$; Figure 3c). Below MAT, temperature increases had positive or no effects on survival (82% of cases) and reproduction (100% of cases), whereas temperature increases above MAT tended to have negative effects on these fitness metrics (81% and 60% of cases, respectively), with the magnitude of sensitivity in survival varying by taxa (Figure 3, a and b). Thermal sensitivity in growth was weak but generally positive both below MAT (100% of cases) and above MAT (58% of cases; Figure 3c). MAT consistently predicted the direction of

thermal sensitivity regardless of whether taxa were acclimated prior to the experiment (WebFigure 2).

As the magnitude of the difference between the experimental temperature and MAT (TRT–MAT) increased above MAT, sensitivity in multiple fitness metrics became more negative, though the shape of this relationship varied by metric and taxonomic group (WebPanel 2; Figure 4). Treatment temperatures within 5–8°C of MAT did not affect algal survival, but algal survival decreased when temperatures were $\geq 10^\circ\text{C}$ above MAT (ie negative sensitivity; quadratic TRT–MAT $F_{1,16} = 4.86$, $P = 0.04$; Figure 4c). In contrast, invertebrate survival declined most when temperatures were $\geq 20^\circ\text{C}$ above MAT (quadratic TRT–MAT $F_{1,209} = 120.01$, $P < 0.001$; Figure 4c). Algal reproduction (quadratic TRT–MAT $F_{1,13} = 21.91$, $P < 0.001$; Figure 4d) and plant growth (linear TRT–MAT $F_{1,9} = 58.98$, $P < 0.001$; WebFigure 3b) were most negatively affected by treatment temperatures approximately 10°C above MAT.

For temperature increases above MAT, latitude predicted population sensitivity in survival (Figure 4a), reproduction (Figure 4b), and growth (WebFigure 3a), but the shape (linear or quadratic) of these relationships varied (WebPanel 2). Invertebrate populations between latitudes of 30–45°N were more likely to be harmed by temperature increases than populations between latitudes of 45–60°N in terms of survival (quadratic latitude $F_{1,209} = 44.23$, $P < 0.001$; Figure 4a) and reproduction (linear latitude $F_{1,20} = 47.28$, $P < 0.001$; Figure 4b). In contrast, algal populations from higher latitudes experienced increasingly negative impacts of warming on survival (linear latitude $F_{1,16} = 11.06$, $P = 0.004$; Figure 4a) and reproduction (quadratic latitude $F_{1,13} = 16.99$, $P = 0.001$; Figure 4b). Temperature increases had relatively little effect on growth rates of all taxa, although algal growth declined with increasing temperature for populations from higher latitudes (linear latitude $F_{1,67} = 39.95$, $P < 0.001$; WebFigure 3a). Population seasonality, a measure of temperature variability, also predicted fitness responses to temperature increases above MAT (WebPanel 2), most notably for algae, with general declines in

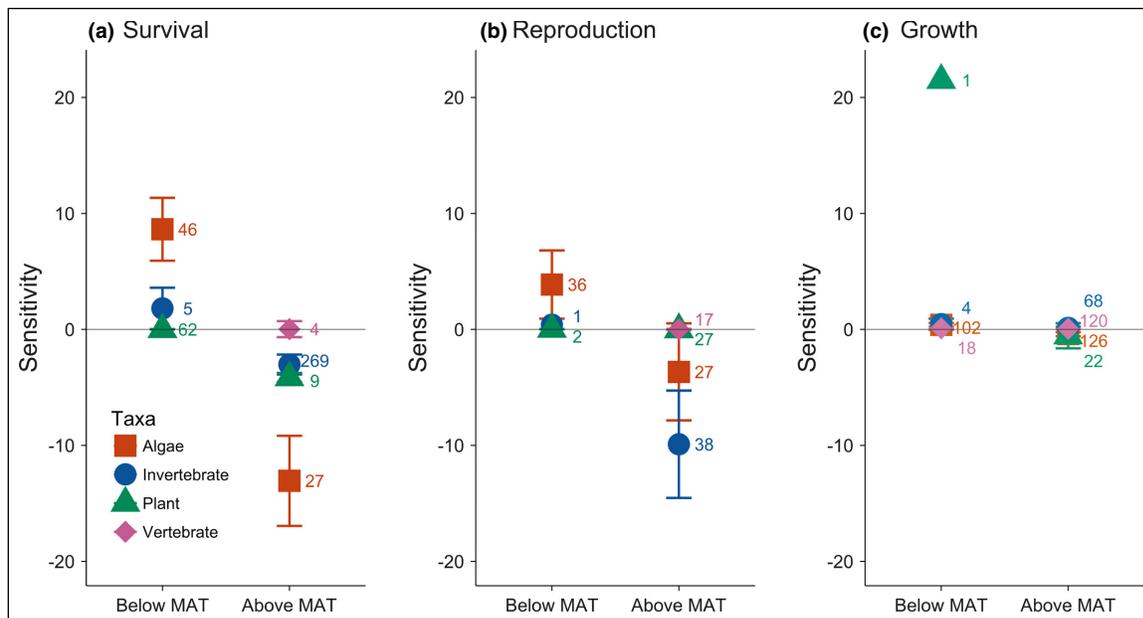


Figure 3. Sensitivity (mean $S \pm 95\%$ CI) in (a) survival, (b) reproduction, and (c) growth to temperature increases below and above population mean annual temperature (MAT). Positive or negative sensitivity indicates positive or negative fitness response (respectively) with increasing temperature. Numbers indicate sample size.

algal survival (linear seasonality $F_{1,16} = 5.81$, $P = 0.02$), reproduction (linear seasonality $F_{1,13} = 13.00$, $P = 0.003$), and growth (linear seasonality $F_{1,67} = 67.92$, $P < 0.001$) as seasonality increased (WebFigure 4). Greater seasonality was also associated with slight increases in growth for plants (quadratic seasonality $F_{1,9} = 54.48$, $P < 0.001$) and invertebrates (linear seasonality $F_{1,36} = 9.80$, $P = 0.003$; WebFigure 4).

Population identity influenced thermal sensitivity, with significant population-level variation in fitness metrics for algae (growth $F_{40,67} = 3.05$, $P < 0.001$; reproduction $F_{5,13} = 5.58$, $P = 0.005$), invertebrates (growth $F_{22,36} = 2.51$, $P = 0.006$; reproduction $F_{9,20} = 3.85$, $P = 0.005$), and plants (reproduction $F_{7,13} = 7.85$, $P < 0.001$; WebPanel 2; WebFigure 5). Species identity was also significant for invertebrates (survival $F_{2,209} = 9.76$, $P < 0.001$) and algae (growth $F_{4,67} = 4.51$, $P = 0.002$; WebPanel 2). When sufficient data were available for its inclusion, life-history stage (ie juvenile versus adult) was also found to predict thermal sensitivity (invertebrate survival $F_{1,209} = 209.81$, $P < 0.001$; invertebrate growth $F_{1,36} = 44.71$, $P < 0.001$; plant growth $F_{1,9} = 118.08$, $P < 0.001$; WebPanel 2; WebFigure 6), results similar to those of Boyd *et al.* (2016).

Discussion

Although organismal responses to a warming planet will depend on a complex suite of intrinsic and extrinsic factors and biotic interactions, understanding the thermal sensitivity of fitness remains fundamental to predicting these responses (Williams *et al.* 2008; Huey *et al.* 2012; Nadeau *et al.* 2017). Here, we demonstrate that a simple metric – MAT – is broadly predictive of the sensitivity of individual fitness responses of marine populations. Temperature increases above

MAT lower survivorship and reproduction of marine populations, whereas temperature increases below MAT enhance survivorship, reproduction, and growth. In addition, temperature change relative to MAT integrates both species sensitivity and exposure to climate change to provide an approximation of vulnerability at the population level (Williams *et al.* 2008; Nadeau *et al.* 2017). Although MAT is not a perfect metric of local thermal environments (Huey *et al.* 2012), its ready availability makes it a valuable first-order approximation for predicting response to temperature change for a wide variety of marine taxa.

Across taxa, growth rates rarely decreased in response to increased temperature (ie “hotter is better” sensu Kingsolver and Huey 2008). Although seemingly a cause for optimism, the dearth of negative effects of increased temperature on growth likely reflects the fact that populations must survive in order to grow, which reinforces the need to measure multiple fitness responses. Indeed, we found clear evidence that temperature increases can cause decreased survival and reproduction, especially when treatment temperatures increased above MAT (Figure 4, c and d). These results highlight the importance of relative, rather than absolute, temperature change for organismal fitness (Deutsch *et al.* 2008). Trade-offs in fitness metrics (eg growth versus reproduction) are not explicitly captured by our analyses because surprisingly few studies of marine near-shore species assessed the effects of non-lethal temperatures on multiple proxies of fitness.

Although latitudinal trends in the thermal tolerances of marine taxa are less pronounced than in terrestrial taxa (Sunday *et al.* 2012), latitude was found to be a significant predictor of sensitivity to warming for all fitness responses when treatment temperatures were above MAT. Invertebrate populations inhab-

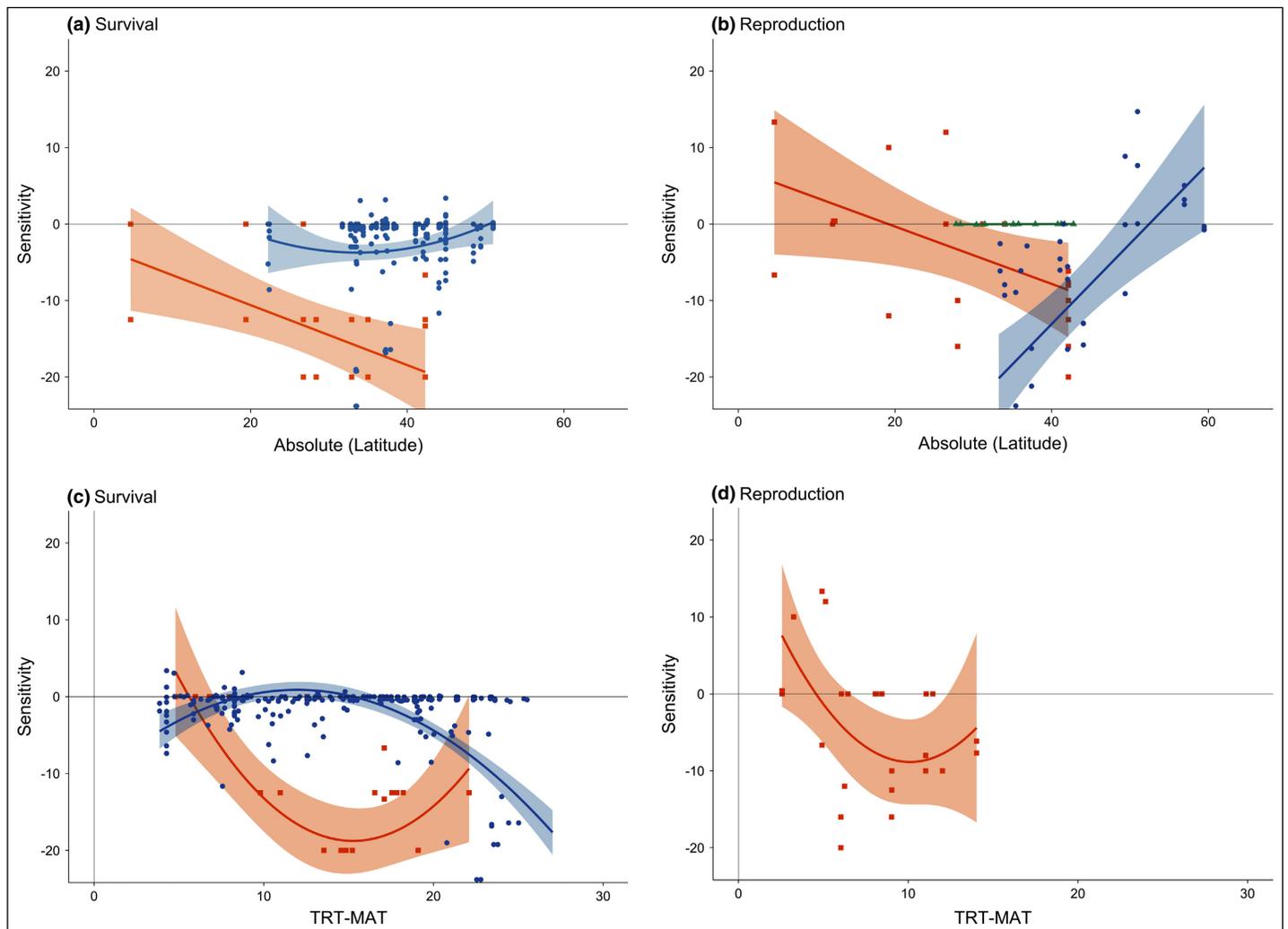


Figure 4. Sensitivity (linear or quadratic fit \pm 95% CI) by (a and b) absolute value of population latitude and (c and d) the difference between experimental treatment temperature and population mean annual temperature (TRT–MAT) for survival (a and c) and reproduction (b and d). Only taxa for which latitude and/or TRT–MAT were significant predictors are depicted (ie vertebrates are not included). Symbols are the same as in Figure 3: orange squares = algae; blue circles = invertebrates; green triangles = plants.

iting latitudes of 30–45°N were more likely to be harmed by temperature increases than populations at higher latitudes (45–60°N; Figure 4, a and b), and populations with higher seasonality (a hallmark of mid-latitude populations) exhibited lowered fitness responses with increases in temperature (WebFigure 4). These results are consistent with previous research showing that mid-latitude terrestrial insects experienced greater reductions in fitness due to warming (Kingsolver *et al.* 2013), and that subtropical regions are vulnerable to warming-related species loss because of thermal bias (Stuart-Smith *et al.* 2015). Our study offers insights into how populations and taxonomic groups tend to respond to temperature increases. However, our interpretation is tempered by the relatively low number of non-lethal fitness experiments involving tropical populations, particularly taxa other than algae (WebPanel 1), even though previous reviews indicated that low-latitude populations may be close to their thermal limits (Deutsch *et al.* 2008) and therefore most at risk (Comte and Olden 2017).

Our analysis included primarily shallow water species that span the gradient from intertidal to subtidal zones. The constant water temperatures maintained throughout most experiments may exaggerate the negative impacts of higher ocean temperatures, particularly for coastal and nearshore populations that experience considerable thermal variability (Helmuth *et al.* 2006; Reusch 2014; Boyd *et al.* 2016). However, because coastal populations are likely to be more tolerant of warming due to frequent exposure to variable conditions (Reusch 2014; Nadeau *et al.* 2017), the negative fitness impacts of temperature increases on the majority of marine species may be even greater. Moreover, exposure of intertidal populations to air temperatures may complicate predictions based solely on seawater MAT (Helmuth *et al.* 2006; Sunday *et al.* 2012), which further supports the idea that manipulations incorporating more realistic temperature regimes are needed (Helmuth *et al.* 2006; Vasseur *et al.* 2014; Boyd *et al.* 2016).

Effectively mitigating climate-change impacts requires methods that predict the vulnerability of populations, prioritize among them, and then implement management strategies for those most at risk (Williams *et al.* 2008; Huey *et al.* 2012; Pacifici *et al.* 2015). MAT provides a robust metric for predicting the direction of marine populations' sensitivity to temperature increases, and this has important implications for the management of such populations in response to climate change. For instance, this approach reveals significant variation across taxonomic groups in their response to temperature increases that occur with extrinsic factors such as seasonality and latitude. In addition, our analysis highlights the distinction between the effects of increases in summer versus winter temperatures: increasing summer temperatures (above MAT) can have strong negative effects on survival and reproduction, whereas increases in winter temperatures (below MAT) have negligible or even positive effects. Populations that reproduce in the summer will be particularly susceptible to negative effects of warming on reproduction. Such insights make it possible to prioritize these populations for management interventions (Pacifici *et al.* 2015). Our results also suggest that species in regions in which warming is most pronounced in winter (Grimm *et al.* 2013) may be more resilient to climate change and could therefore be the focus of protection efforts (McLeod *et al.* 2009). Finally, observed shifts in the strength and direction of sensitivity to temperature increases above MAT across latitude and with seasonality support the notion that populations have the evolutionary potential to adapt to profound shifts in temperatures (Bell and Collins 2008; Nadeau *et al.* 2017). For many reasons, however, it remains uncertain whether such evolutionary "rescue" can really sustain populations over time (Kelly *et al.* 2012; see Calosi *et al.* [2016] for review). As such, our approach reinforces the need to consider connectivity among populations in systematic conservation plans, including the location of marine protected areas (McLeod *et al.* 2009; Nadeau *et al.* 2017).

Acknowledgements

We thank S Shuster and T Whitham for conversations that inspired these analyses, and T Schulte for constructive feedback on a prior version of the manuscript. Funding was provided by the US National Science Foundation DEB-1556738 to ARH and OCE-1357386 to EES. This is contribution 383 from the Northeastern University Marine Science Center.

References

- Angert AL, Sheth SN, and Paul JR. 2011. Incorporating population-level variation in thermal performance into predictions of geographic range shifts. *Integr Comp Biol* **51**: 733–50.
- Araújo MS, Ferri-Yanez F, Bozinovic F, *et al.* 2013. Heat freezes niche evolution. *Ecol Lett* **16**: 1206–19.
- Banzon V, Reynolds R, and National Center for Atmospheric Research Staff (Eds). 2014. The climate data guide: SST data: NOAA high-resolution (0.25×0.25) blended analysis of daily SST and ice, OISSTv2. Boulder, CO: National Center for Atmospheric Research. <https://climatedataguide.ucar.edu/climate-data/sst-data-noaa-high-resolution-025x025-blended-analysis-daily-sst-and-ice-oisstv2>. Viewed 4 Jun 2018.
- Bell G and Collins S. 2008. Adaptation, extinction and global change. *Evol Appl* **1**: 3–16.
- Boyd PW, Cornwall CE, Davison A, *et al.* 2016. Biological responses to environmental heterogeneity under future ocean conditions. *Glob Change Biol* **22**: 2633–50.
- Calosi P, De Wit P, Thor P, and Dupont S. 2016. Will life find a way? Evolution of marine species under global change. *Evol Appl* **9**: 1035–42.
- Comte L and Olden JD. 2017. Climatic vulnerability of the world's freshwater and marine fishes. *Nat Clim Change* **7**: 718–22.
- Davis MB, Shaw RG, and Etterson JR. 2005. Evolutionary responses to changing climate. *Ecology* **86**: 1704–14.
- Dawson TP, Jackson ST, House JI, *et al.* 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* **332**: 53–58.
- Deutsch CA, Tewksbury JJ, Huey RB, *et al.* 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *P Natl Acad Sci USA* **105**: 6668–72.
- Diffenbaugh NS and Field CB. 2013. Changes in ecologically critical terrestrial climate conditions. *Science* **341**: 486–92.
- Foden WB, Butchart SHM, Stuart SN, *et al.* 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE* **8**: e65427.
- Forster J, Hirst AG, and Woodward G. 2011. Growth and development rates have different thermal responses. *Am Nat* **178**: 668–78.
- Gaitan-Espitia JD, Bacigalupe LD, Opitz T, *et al.* 2014. Geographic variation in thermal physiological performance of the intertidal crab *Petrolisthes violaceus* along a latitudinal gradient. *J Exp Biol* **217**: 4379–86.
- Grimm NB, Chapin III FS, Bierwagen B, *et al.* 2013. The impacts of climate change on ecosystem structure and function. *Front Ecol Environ* **11**: 474–82.
- Helmuth B, Mieszkowska N, Moore P, and Hawkins SJ. 2006. Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. *Annu Rev Ecol Evol S* **37**: 373–404.
- Huey RB, Kearney MR, Krockenberger A, *et al.* 2012. Predicting organismal vulnerability to climate warming: roles of behavior, physiology and adaptation. *Philos T Roy Soc B* **367**: 1665–79.
- Huey RB and Kingsolver JG. 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol Evol* **4**: 131–35.
- Huey RB and Stevenson RD. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am Zool* **19**: 357–66.
- IPCC (Intergovernmental Panel on Climate Change). 2014. Annex II: glossary. In: Barros VR, Field CB, Dokken DJ, *et al.* (Eds). Climate Change 2014: impacts, adaptation, and vulnerability. Part B: regional aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK, and New York, NY: Cambridge University Press.
- Kelly MW, Sanford E, and Grosberg RK. 2012. Limited potential for adaptation to climate change in a broadly distributed marine crustacean. *P Roy Soc B-Biol Sci* **279**: 349–56.

- Kingsolver JG, Diamond SE, and Buckley LB. 2013. Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Funct Ecol* **27**: 1415–23.
- Kingsolver JG and Huey RB. 2008. Size, temperature, and fitness: three rules. *Evol Ecol Res* **10**: 251–68.
- Kinne O. 1960. Growth, food intake, and food conversion in a euryplastic fish exposed to different temperatures and salinities. *Physiol Zool* **33**: 288–317.
- Laffoley D and Baxter JM. 2016. Explaining ocean warming: causes, scale, effects, and consequences. Gland, Switzerland: International Union for Conservation of Nature.
- McLeod E, Salm R, Green A, and Almany J. 2009. Designing marine protected area networks to address the impacts of climate change. *Front Ecol Environ* **7**: 362–70.
- Nadeau CP, Urban MC, and Bridle JR. 2017. Climates past, present, and yet-to-come shape climate change vulnerabilities. *Trends Ecol Evol* **32**: 786–800.
- Pacifici M, Foden WB, Visconti P, *et al.* 2015. Assessing species vulnerability to climate change. *Nat Clim Change* **5**: 215–24.
- Parmesan C and Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.
- Pierce D. 2015. ncd4: interface to Unidata netCDF data files. R package v1.6.9. Vienna, Austria: The R Foundation. <https://cran.r-project.org/web/packages/ncdf4/ncdf4.pdf>. Viewed 19 Nov 2018.
- Portner H-O, Karl DM, Boyd PW, *et al.* 2014. Ocean systems. In: Field CB, Barros VR, Dokken DJ, *et al.* (Eds). Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press.
- R Core Team. 2018. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. www.R-project.org.
- Reusch TBH. 2014. Climate change in the oceans: evolutionary versus phenotypically plastic responses of marine animals and plants. *Evol Appl* **7**: 104–22.
- Sheldon KS and Tewksbury JJ. 2014. The impact of seasonality in temperature on thermal tolerance and elevational range size. *Ecology* **95**: 2134–43.
- Sinclair BJ, Marshall KE, Sewell MA, *et al.* 2016. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecol Lett* **19**: 1372–85.
- Stuart-Smith RD, Edgar GJ, Barrett NS, *et al.* 2015. Thermal biases and vulnerability to warming in the world's marine fauna. *Nature* **528**: 88–92.
- Stuart-Smith RD, Edgar GJ, and Bates AE. 2017. Thermal limits to the geographic distributions of shallow-water marine species. *Nature Ecol Evol* **1**: 1846.
- Sunday JM, Bates AE, and Dulvy NK. 2012. Thermal tolerance and the global redistribution of animals. *Nat Clim Change* **2**: 686–90.
- Sunday JM, Bates AE, Kearney MR, *et al.* 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *P Natl Acad Sci USA* **111**: 5610–15.
- Thomas MK, Kremer CT, and Litchman E. 2016. Environment and evolutionary history determine the global biogeography of phytoplankton temperature traits. *Global Ecol Biogeogr* **25**: 75–86.
- Vasseur DA, DeLong JP, Gilbert B, *et al.* 2014. Increased temperature variation poses a greater risk to species than climate warming. *P Roy Soc B-Biol Sci* **281**: 20132612.
- Williams SE, Shoo LP, Isaac JL, *et al.* 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol* **6**: 2621–25.
- Wu Z, Dijkstra P, Koch GW, *et al.* 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Glob Change Biol* **17**: 927–42.

■ Supporting Information

Additional, web-only material may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/fee.1986/supinfo>