

Research



Cite this article: Sasaki M, Hedberg S, Richardson K, Dam HG. 2019 Complex interactions between local adaptation, phenotypic plasticity and sex affect vulnerability to warming in a widespread marine copepod. *R. Soc. open sci.* **6**: 182115. <http://dx.doi.org/10.1098/rsos.182115>

Received: 11 December 2018

Accepted: 27 February 2019

Subject Category:

Biology (whole organism)

Subject Areas:

ecology/evolution

Keywords:

thermal adaptation, climate change, copepod, sex-specific response, developmental plasticity, *Acartia tonsa*

Author for correspondence:

Matthew Sasaki

e-mail: matthew.sasaki@uconn.edu

Complex interactions between local adaptation, phenotypic plasticity and sex affect vulnerability to warming in a widespread marine copepod

Matthew Sasaki¹, Sydney Hedberg², Kailin Richardson³ and Hans G. Dam¹

¹Department of Marine Sciences, University of Connecticut, Groton, CT, USA

²Gustavus Adolphus College, St Peter, MN 56082, USA

³Savannah State University, Savannah, GA 31404, USA

MS, 0000-0001-5560-5363; HGD, 0000-0001-6121-5038

Predicting the response of populations to climate change requires an understanding of how various factors affect thermal performance. Genetic differentiation is well known to affect thermal performance, but the effects of sex and developmental phenotypic plasticity often go uncharacterized. We used common garden experiments to test for effects of local adaptation, developmental phenotypic plasticity and individual sex on thermal performance of the ubiquitous copepod, *Acartia tonsa* (Calanoida, Crustacea) from two populations strongly differing in thermal regimes (Florida and Connecticut, USA). Females had higher thermal tolerance than males in both populations, while the Florida population had higher thermal tolerance compared with the Connecticut population. An effect of developmental phenotypic plasticity on thermal tolerance was observed only in the Connecticut population. Our results show clearly that thermal performance is affected by complex interactions of the three tested variables. Ignoring sex-specific differences in thermal performance may result in a severe underestimation of population-level impacts of warming because of population decline due to sperm limitation. Furthermore, despite having a higher thermal tolerance, low-latitude populations may be more vulnerable to warming as they lack the ability to respond to increases in temperature through phenotypic plasticity.

1. Introduction

Temperature has a profound effect on organismal performance [1,2]. Rapid climate warming represents a significant challenge for organisms, increasing average environmental temperatures [3] and the frequency of extreme climatic events such as heat waves [4]. Predicting organismal responses to these changes depends on our understanding of the factors affecting thermal tolerance. Acute thermal tolerance is known to be affected by phenotypic plasticity [5] and genetic differentiation [6], as well as diet, behaviour and individual sex [7–9]. Spatial variation in the thermal environment should generate adaptive differences in thermal performance between populations from different environments [2].

Copepods are arguably the most abundant metazoan on the planet [10]. Thus, they are intimately linked to all commercial fisheries and to global biogeochemical cycles [11]. Copepods occupy diverse ecological niches and habitat types, adopting a wide range of lifestyles. Because of their ecological importance, short-generation time and ability to being cultured in the laboratory, copepods are ideal candidates for studying adaptation to aquatic environments. Many copepod taxa have large geographical ranges, encompassing a large degree of variation in the thermal environment; thus, predicting their response to warming will be population-dependent and strongly influenced by specialist-generalist trade-offs in performance [12].

The climate variability hypothesis (CVH) [13,14] states that increased thermal tolerance should correspond with increased mean environmental temperature, while plasticity should evolve in response to variability in the thermal environment. These predictions are broadly supported in terrestrial and freshwater aquatic systems [15,16], but support in marine systems is limited by a paucity of studies [17–19], particularly in widely dispersed pelagic organisms. Moreover, these studies have generally not explicitly addressed the role of developmental phenotypic plasticity or sex-specific thermal performance. Both of these have been documented for a variety of taxa [8,17,20,21] including copepods [9,19,22,23]. Developmental phenotypic plasticity is likely an important mechanism organisms use to cope with variation in environmental conditions [24]. Sex-specific differences in organismal performance are also likely to be important in determining the outcomes of climate change. There is emerging evidence, for example, that sex-specific performance may play a large role in determining organismal responses to ocean acidification [25]. Combined with possible sperm limitation in copepod populations [26,27], this suggests that sex-specific differences in thermal adaptation are an important factor to consider in the determination of copepod vulnerability to warming, as well as for predictions based on the CVH.

Acartia tonsa is a widely distributed calanoid copepod, which dominates coastal and estuarine systems around the globe [28,29]. This species is characterized by relatively short generation times of the order of weeks [30–33]. There is distinct sexual dimorphism, with females being considerably larger than males. Body size is generally temperature-dependent in copepods [34,35]. In *A. tonsa*, mature females are typically less than 1 mm in length, with males averaging around 0.7 mm [36]. Unlike larger calanoids, *A. tonsa* does not maintain large lipid energy reserves [37]. With a geographical range covering a large latitudinal thermal gradient in the North Atlantic, this is a good model system to explore the contributions of various adaptive mechanisms to thermal adaptation [19]. Here, we examine the effects of genetic differentiation, developmental phenotypic plasticity and individual sex on thermal tolerance and body size in the copepod *A. tonsa*. Our results show that complex interactions between these variables strongly affect our ability to predict organismal responses to climate change.

2. Methods

Plankton samples were collected with surface tows at field sites in Groton, Connecticut, and Punta Gorda, Florida (table 1), during July and August 2017 using a 250 µm mesh plankton net and non-filtering cod end. Sea surface temperature data for both sites (table 1) were obtained from the AQUA-MODIS satellite database [38]. Both sampling locations were in shallow water (less than 2 m); thus, surface temperature data are likely a good representation of temperature throughout the water column. Connecticut represents a cool, more variable thermal environment compared with Florida, which is characterized by warm and stable temperatures. Daily temperature variation at each site is minor compared with the inter-site differences [39]. Initial laboratory populations of more than 1500 mature adults were established from collected animals. Cultures were maintained in 0.6 µm filtered

Table 1. Site name, geographical coordinates, mean annual temperature, mean annual maximum and mean annual temperature range for all collection locations.

population	coordinates (latitude, longitude)	mean annual temperature (°C)	mean annual maximum temperature (°C)	mean annual temperature range (°C)
Connecticut (CT)	41.320591 N, −72.001564 W	13.3	22.7	22.5
Florida (FL)	26.940398 N, −82.051036 W	24.9	31.4	15.3

seawater under common garden conditions (salinity: 30 practical salinity units, 12 h : 12 h light : dark, 18°C) for several generations. During this time, copepods were fed ad libitum a diet of the microalgae *Tetraselmis* sp., *Rhodomonas* sp. and *Thalassiosira weissflogii*, which were semi-continuously cultured in F/2 medium (F/2 – silicate for *Tetraselmis* sp. and *Rhodomonas* sp.) under the same conditions. Cultures were maintained under these conditions for several generations before the experiments, thus minimizing the effects of previous environmental acclimation (i.e. differences in food abundance/quality and temperature) in the field.

Body size measurements were taken for individuals from the laboratory cultures ($n = 30$ males and 30 females for both sexes from both populations). Individuals were isolated in a drop of filtered seawater and photographed using a camera attached to an inverted microscope after the water had been removed. Body lengths were measured as the length of the prosome using Image-J (<https://imagej.nih.gov/ij/>).

To test for the effect of developmental temperature, a fraction of the eggs from the 18°C culture were moved to 22°C to develop. All other variables were held constant. Once mature, individuals from both developmental conditions (18 and 22°C) were exposed to a 24 h acute heat stress. Individuals were carefully transferred to a microcentrifuge tube filled with 1.5 ml of filtered seawater, then transferred to heat blocks set to a constant temperature (18–38°C at 1°C intervals). Each individual experienced a single temperature. Individual survivorship was recorded after 24 h as binary data (1, survival; 0, mortality). Survivorship was determined during examination under a dissection microscope by response to stimuli or visible gut-passage movement. A total of 1717 individuals were used throughout the experiments (727 CT individuals and 990 FL individuals). Initial heat stresses were performed across the entire range of temperatures (18–38°C) in order to determine where additional heat stresses were needed for each of the populations. Therefore, different numbers of individuals were used for the two populations as the two temperature ranges differed between the populations.

All analyses were performed using the software package R v. 3.5.1 [40]. Body size measurements were analysed using a three-way ANOVA (body size ~ population * developmental temperature * sex). A Levene's test was used to test the assumption of homogeneity of variance. A Tukey post hoc test was then used to examine pairwise differences between the various groups. To analyse the survivorship data, an initial ANOVA was run for all data (survivorship ~ stress temperature + sex + developmental temperature + population, and all two-way interactions). Three-way and four-way interactions were excluded. ANOVAs were also run for each population separately (survivorship ~ stress temperature * sex * developmental temperature). Thermal performance curves were estimated using logistic regressions on the data from both developmental temperatures from both populations. Because of the common garden design, differences in the performance curves between developmental conditions within a population can be attributed to developmental phenotypic plasticity, whereas differences between populations should reflect the effects of genetic differentiation. LD₅₀ (the temperature with 50% mortality) was calculated for each performance curve. The change in LD₅₀ between the two developmental conditions (Δ LD₅₀) was used as a measure of the magnitude of the plastic response.

3. Results

3.1. Body size

Female copepods were always significantly larger than males, regardless of population or developmental temperature (figure 1, $p < 2.2 \times 10^{-16}$). Both male and female copepods from the CT population were significantly larger than copepods from the FL population in the 18°C developmental treatment

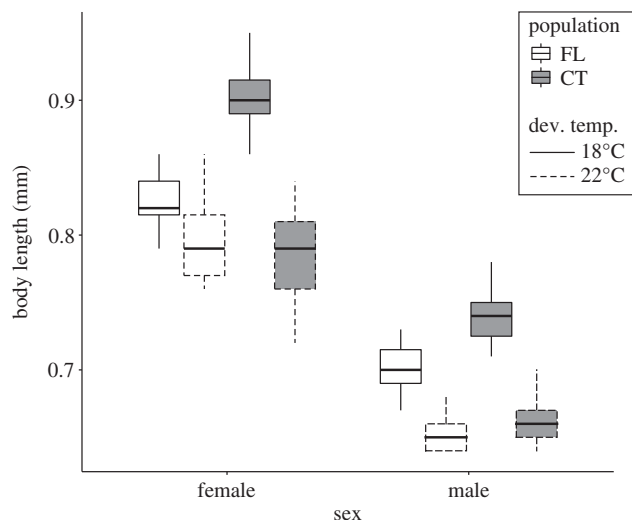


Figure 1. A box-and-whisker plot showing body size data for the various groups. Measurements are grouped by sex. The Florida (FL) population is shown in white, and the Connecticut (CT) population in grey. The two developmental temperature groups (18 and 22°C) are indicated with solid and dashed lines, respectively.

($p < 2.874 \times 10^{-10}$). However, there were no significant differences between the respective sexes from the CT and FL populations in the 22°C developmental treatment. Both populations saw a significant reduction in body length with an increase in developmental temperature ($p < 2.2 \times 10^{-16}$).

3.2. Genetic differentiation

We observed clear differences between performance curves for the two populations, consistent with a significant population effect in the full ANOVA (table 2). The Florida (FL) population performance curve was shifted towards warmer temperatures compared with the Connecticut (CT) population (figure 2). This is also reflected in the reaction norms (figure 3); FL individuals had a higher thermal tolerance than individuals of the same sex from the CT population.

3.3. Developmental phenotypic plasticity

The observed significant developmental temperature \times population interaction term in the full ANOVA suggests that the effect of developmental temperature differed between the two populations (table 2). The ANOVA results for the CT population showed a significant effect of developmental temperature which was not observed for the FL population. Thermal performance curves for the 18 and 22°C developmental temperature treatments differed in CT but not FL individuals (figure 2, dashed versus solid lines). The slope of the reaction norms, which represents the magnitude of developmental phenotypic plasticity (figure 3), was not significantly different from zero for FL individuals, regardless of sex. By contrast, slopes of the reaction norms for both sexes in the CT population were significantly greater than zero ($p = 0.001202$).

3.4. Sex-dependent thermal performance traits

Males showed significantly lower survival than females in both populations (figure 2, red versus blue lines). LD_{50} reaction norms also showed clear sex-dependent differences in thermal tolerance (figure 3), with females being always more tolerant than males. However, there were no sex-dependent differences in the plastic response between males and females (no Sex \times Dev. Temp. interaction term in the full ANOVA), regardless of population.

4. Discussion

The two populations of *A. tonsa* used in this study were collected from strongly differing thermal environments—Connecticut, a cool, variable environment, and Florida, a warmer, more stable

Table 2. ANOVA results for the logistic regression relating survivorship to stress temperature, population, developmental temperature and individual sex. Significant terms ($p < 0.05$) are shown in *italics*.

	d.f.	deviance	resid. d.f.	resid. dev	Pr(>Chi)
all data					
<i>stress temperature</i>	1	928.89	1715	1409.7	0.00
<i>individual sex</i>	1	54.7	1714	1355	1.40×10^{-13}
<i>developmental temperature</i>	1	7.74	1713	1347.2	0.005388
<i>population</i>	1	17.8	1712	1329.4	2.45×10^{-05}
<i>dev. temp. \times population</i>	1	5.46	1711	1324	0.019462
<i>sex \times dev. temp</i>	1	0.27	1710	1323.7	0.60482
<i>sex \times population</i>	1	3.82	1709	1319.9	0.050578
<i>stress temp. \times population</i>	1	8.38	1708	1311.5	0.003801
<i>stress temp. \times dev. temp.</i>	1	0.06	1707	1311.5	0.809781
<i>stress temp. \times sex</i>	1	2.29	1706	1309.2	0.130522
CT model					
<i>stress temperature</i>	1	318.6	725	666.22	0.00
<i>individual sex</i>	1	29.42	724	636.8	5.82×10^{-8}
<i>developmental temperature</i>	1	10.49	723	626.31	0.001202
<i>stress temp. \times sex</i>	1	0	722	626.31	0.960815
<i>stress temp. \times dev. temp.</i>	1	0.14	721	626.17	0.71148
<i>sex \times dev. temp.</i>	1	0.23	720	625.94	0.631601
<i>stress temp. \times sex \times dev. temp.</i>	1	1.75	719	624.2	0.186143
FL model					
<i>stress temperature</i>	1	646.63	988	706.5	0.00
<i>individual sex</i>	1	20.51	987	685.99	5.94×10^{-6}
<i>developmental temperature</i>	1	0.63	986	685.36	0.42597
<i>stress temp. \times sex</i>	1	4.86	985	680.5	0.02744
<i>stress temp. \times dev. temp.</i>	1	2.97	984	677.52	0.08465
<i>sex \times dev. temp.</i>	1	0.22	983	677.31	0.64267
<i>stress temp. \times sex \times dev. temp.</i>	1	0.23	982	677.08	0.63395

environment. We observed lower thermal tolerance, but stronger plasticity in the CT population relative to the FL population, consistent with expectations of the CVH [13,14]. While the results for both male and female performance are consistent with the CVH, we find that individual sex had the largest effect on thermal tolerance. It is important to emphasize that our study is not a strong test of the CVH, as only two populations were used. However, the clear evidence that genetic differentiation, phenotypic plasticity and individual sex interact to determine thermal tolerance within the framework of the CVH is critical for our understanding of organismal responses to warming. The demographic implications of these results are crucial to consider in predictions of future population dynamics.

Large variation was also observed in the body size data. Females were always larger than males, as is commonly observed in copepods [41,42]. Females and males from the northern (CT) population were larger than their counterparts from the southern (FL) population in the 18°C developmental temperature treatment. Bergmann's rule posits that populations from higher latitudes should have larger body sizes than populations from lower latitudes [43]. Other studies of copepods have also observed body size clines in agreement with this rule [44]. Because of the common garden experimental design, the differences in body size we observed here are likely genetically determined. However, these differences are not observed in the 22°C developmental temperature group, suggesting a more complex interaction between the developmental temperature and genotype.

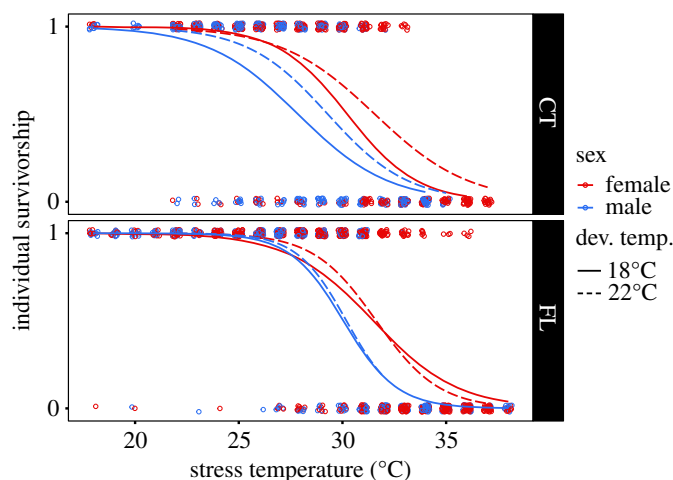


Figure 2. Survivorship data for adult *A. tonsa* individuals are indicated by the points (1, survival; 0, mortality). Thermal performance curves are estimated by logistic regression. Colour and line type indicate individual sex and developmental temperature, respectively.

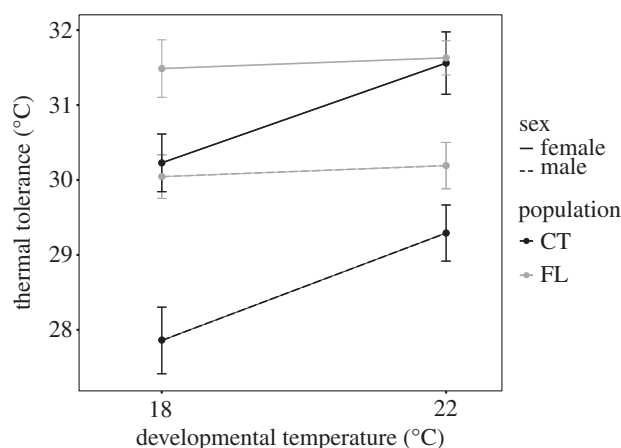


Figure 3. Reaction norms for adult *A. tonsa* showing thermal tolerance (LD_{50}) as a function of developmental temperature for both sexes (line type) from the two populations (colour). Points are thermal tolerance \pm s.e. from the logistic regression models. Reaction norm slope is the magnitude of plasticity.

In both populations, females always had a higher thermal tolerance than males. Sex-specific differences in thermal tolerance are observed across diverse systems [8,9,20,21,45]. Within copepods, the few studies that have examined sex-specific thermal tolerance have also found females to be more thermally tolerant than males [9,22,23,46], but ours is the first to examine these differences in more than one adaptive mechanism (thermal tolerance and phenotypic plasticity), and in multiple populations. Interestingly, female copepods have also been found to be more tolerant to toxic dinoflagellates [47] and to starvation [48,49]. The observations of higher tolerance to diverse stressors in females may be underlain in part by a ‘live fast, die young’ strategy in mate-searching males [50]. Thermal tolerance is also often observed to correlate with smaller body size [43,51–53], although this appears to be strongly species-specific [54]. In our study, smaller body size is observed to correlate with increased thermal tolerance between populations, but not between the sexes; FL copepods are smaller than CT individuals and have a higher thermal tolerance while males are smaller than females but have a lower thermal tolerance.

While there are strong differences in male and female thermal tolerance in this study, neither population exhibits significant differences between male and female plastic capacity (ΔLD_{50}). No previous studies have examined differences in male and female developmental phenotypic plasticity, but higher acclimatory capacity was observed in females of a different copepod species [9]. This difference in sex-dependence of the different adaptive mechanisms (a difference in thermal tolerance but not in phenotypic plasticity between the sexes) suggests that their physiological basis is different.

Multiple factors affect acute thermal stress tolerance. Understanding these factors, and how they vary among populations, has critical implications for predictions of future population dynamics. Lower male thermal tolerance creates an asymmetrical vulnerability to climate change, which could lead to

population declines under less intense warming due to sperm-limitation [27,55]. Our results also suggest that despite having a higher thermal tolerance, low-latitude populations may be more vulnerable to projected warming. That is, the small difference between LD₅₀ values and average annual maximum temperature indicates that copepods in these regions are near their thermal limit under present conditions. As they are also unable to respond to increased temperatures through developmental phenotypic plasticity, any further increase in temperature is likely to have deleterious effects on population survival, as previously suggested for tropical copepods [12,56]. Furthermore, males have a significantly lower thermal tolerance, further lowering the temperature threshold that would bring the onset of temperature-driven population dynamic changes. Both sexes in the CT population, however, have thermal tolerance values well above the current temperature maximum, and have a robust plastic capacity to increase thermal tolerance, potentially decreasing deleterious effects of warming on this population. Contemporary thermal tolerance and phenotypic plasticity are just two of the determinants of vulnerability to climate change. Rapid adaptation to changing climate may also affect population vulnerability [57,58]. In that regard, our results suggest that temperature-driven selective pressure may be different for the two sexes. The implications of this for the evolutionary dynamics of thermal adaptation are largely unexplored [59].

Ultimately, thermal tolerance and the mechanisms affecting it are only components of the suite of factors that will determine vulnerability to climate change. While genetic differentiation and phenotypic plasticity are two of the major adaptive mechanisms, behaviour may also play a large role in response to warming [60,61]. Avoidance of adverse conditions and range shifts are also possible, especially in planktonic organisms [62,63]. Further, there are ecological effects of warming such as changing patterns of primary productivity [64–66] as well as changes in predator–prey interactions [67–70]. Phenological mismatches between copepods, their prey and their predators, for example, could also have profound effects on marine communities [71,72]. These ecological factors could interact with warming directly; food availability has been shown to affect thermal tolerance in other organisms [73–76]. It is clear that multiple adaptive mechanisms and factors will determine vulnerability to climate change. We show here that among these factors, genetic differentiation, phenotypic plasticity and individual sex have significant, population-specific influences on thermal tolerance. Hence, they should be taken into consideration in a wider range of model systems.

Data accessibility. Sasaki MC, Hedberg S, Richardson K, Dam HG. Data from: Complex interactions between local adaptation, plasticity, and sex determine vulnerability to warming in a widespread marine copepod. Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.v5g6r80>.

Authors' contributions. H.G.D. and M.S. designed the study. M.S. collected and cultured all copepods. K.R. and S.H. performed the experiments. M.S. analysed the data. M.S. and H.G.D. drafted the manuscript. All authors read and approved the manuscript.

Competing interests. We have no competing interests.

Funding. Supported by NSF grants 1559180 and 1658663, a Research Council grant from the University of Connecticut, and graduate research fellowships from the Department of Marine Sciences, University of Connecticut, USA.

Acknowledgements. S.H. and K.R. were participants in the UCONN-Mystic Aquarium Research Experience for Undergraduates program (<http://www.mysticaquarium.org/reu/>). We thank Drs Tracy Romano and Michael Finiguerra for organizing and leading this programme.

References

- Hochachka PW, Somero GN. 2002 *Biochemical adaptation: mechanism and process in physiological evolution*. New York, NY: Oxford University Press.
- Angilletta MJ. 2009 *Thermal adaptation: a theoretical and empirical analysis*. New York, NY: Oxford University Press.
- Pachauri RK et al. 2014 *Climate change 2014: synthesis report*. In Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: IPCC.
- Meehl GA. 2004 More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* **305**, 994–997. (doi:10.1126/science.1098704)
- Stillman JH. 2003 Acclimation capacity underlies susceptibility to climate change. *Science* **301**, 65. (doi:10.1126/science.1083073)
- Hochachka PW, Somero GN. 1968 The adaptation of enzymes to temperature. *Comp. Biochem. Physiol.* **27**, 659–668. (doi:10.1016/0010-406X(68)90605-1)
- Andersen LH, Kristensen TN, Loeschcke V, Toft SR, Mayntz D. 2010 Protein and carbohydrate composition of larval food affects tolerance to thermal stress and desiccation in adult *Drosophila melanogaster*. *J. Insect. Physiol.* **56**, 336–340. (doi:10.1016/j.jinsphys.2009.11.006)
- Johnstone M, Schiffer M, Hoffmann AA. 2017 Separating multiple sources of variation on heat resistance in *Drosophila hydei*. *J. Insect. Physiol.* **96**, 122–127. (doi:10.1016/j.jinsphys.2016.11.001)
- Bradley BP. 1978 Increase in range of temperature tolerance by acclimation in the copepod *Eurytemora affinis*. *Biol. Bull.* **154**, 177–187. (doi:10.2307/1541120)
- Humes AG. 1994 How many copepods? *Hydrobiologia* **292**, 1–7. (doi:10.1007/BF00229916)
- Miller CB, Wheeler PA. 2012 *Biological oceanography*. Hoboken, NJ: John Wiley & Sons.
- Dam HG. 2013 Evolutionary adaptation of marine zooplankton to global change. *Annu.*

- Rev. Mar. Sci. **5**, 349–370. (doi:10.1146/annurev-marine-121211-172229)
13. Janzen DH. 1967 Why mountain passes are higher in the tropics. *Am. Nat.* **101**, 233–249. (doi:10.1086/282487)
 14. Stevens GC. 1989 The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat.* **133**, 240–256. (doi:10.1086/284913)
 15. Shah AA *et al.* 2017 Climate variability predicts thermal limits of aquatic insects across elevation and latitude. *Funct. Ecol.* **31**, 2118–2127. (doi:10.1111/1365-2435.12906)
 16. Sunday JM, Bates AE, Dulvy NK. 2011 Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B* **278**, 1823–1830. (doi:10.1098/rspb.2010.1295)
 17. Stillman JH, Somero GN. 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. (doi:10.1086/316738)
 18. Compton TJ, Rijkenberg MJA, 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. (doi:10.1016/j.jembe.2007.07.010)
 19. Pereira RJ, Sasaki MC, Burton RS. 2017 Adaptation to a latitudinal thermal gradient within a widespread copepod species: the contributions of genetic divergence and phenotypic plasticity. *Proc. R. Soc. B* **284**, 20170236–20170238. (doi:10.1098/rspb.2017.0236)
 20. Jeffries KM, Hinch SG, Martins EG, Clark TD, Lotto AG, Patterson DA, Cooke SJ, Farrell AP, Miller KM. 2012 Sex and proximity to reproductive maturity influence the survival, final maturation, and blood physiology of Pacific salmon when exposed to high temperature during a simulated migration. *Physiol. Biochem. Zool.* **85**, 62–73. (doi:10.1086/663770)
 21. Winne CT, Keck MB. 2005 Intraspecific differences in thermal tolerance of the diamondback watersnake (*Nerodia rhombifer*): effects of ontogeny, latitude, and sex. *Comp. Biochem. Physiol. A: Mol. Integr. Physiol.* **140**, 141–149. (doi:10.1016/j.cbpa.2004.11.009)
 22. Willett CS. 2010 Potential fitness trade-offs for thermal tolerance in the intertidal copepod *Tigriopus californicus*. *Evolution* **64**, 2521–2534. (doi:10.1111/j.1558-5646.2010.01008.x)
 23. Hall CJ. 2001 Effects of salinity and temperature on survival and reproduction of *Boeckella hamata* (Copepoda: Calanoida) from a periodically brackish lake. *J. Plankton Res.* **23**, 97–104. (doi:10.1093/plankt/23.1.97)
 24. West-Eberhard MJ. 2003 *Developmental plasticity and evolution*. Oxford, UK: Oxford University Press.
 25. Ellis RP *et al.* 2017 Does sex really matter? Explaining intraspecific variation in ocean acidification responses. *Biol. Lett.* **13**, 20160761. (doi:10.1098/rsbl.2016.0761)
 26. Kiørboe T. 2006 Sex, sex-ratios, and the dynamics of pelagic copepod populations. *Oecologia* **148**, 40–50. (doi:10.1007/s00442-005-0346-3)
 27. Burris Z, Dam HG. 2015 Spermatophore production as a function of food abundance and age in the calanoid copepods, *Acartia tonsa* and *Acartia hudsonica*. *Mar. Biol.* **164**, 841–853. (doi:10.1007/s00227-015-2628-6)
 28. Wilson CB. 1932 The copepods of the Woods Hole region, Massachusetts. *Bull. US Natl Mus.* **158**, 1–635. (doi.org/10.5479/si.03629236.158.1)
 29. Bergmann C. 1848 *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse*. Göttingen, Germany: Vandenhoeck & Ruprecht.
 30. Lonsdale DJ, Levinton JS. 1985 Latitudinal differentiation in copepod growth: an adaptation to temperature. *Ecology* **66**, 1397–1407. (doi:10.2307/1938002)
 31. Blankenhorn WU, Gautier R, Nick M, Puniamoorthy N, Schäfer MA. 2014 Stage- and sex-specific heat tolerance in the yellow dung fly *Scathophaga stercoraria*. *J. Therm. Biol.* **46**, 1–9. (doi:10.1016/j.jtherbio.2014.09.007)
 32. Damgaard RM, Davenport J. 1994 Salinity tolerance, salinity preference and temperature tolerance in the high-shore harpacticoid copepod *Tigriopus brevicornis*. *Mar. Biol.* **118**, 443–449. (doi:10.1007/BF00350301)
 33. Avery DE, Altland KK, Dam HG. 2008 Sex-related differential mortality of a marine copepod exposed to a toxic dinoflagellate. *Limnol. Oceanogr.* **53**, 2627–2635. (doi:10.4319/lo.2008.53.6.2627)
 34. Finiguerra MB, Dam HG, Avery DE, Burris Z. 2013 Sex-specific tolerance to starvation in the copepod *Acartia tonsa*. *J. Exp. Mar. Biol. Ecol.* **446**, 17–21. (doi:10.1016/j.jembe.2013.04.018)
 35. Saiz E, Calbet A, Griffell K. 2017 Sex-dependent effects of caloric restriction on the ageing of an ambush feeding copepod. *Sci. Rep.* **7**, 12662. (doi:10.1038/s41598-017-12661-4)
 36. Bonduriansky R, Maklakov A, Zajitschek F, Brooks R. 2008 Sexual selection, sexual conflict and the evolution of ageing and life span. *Funct. Ecol.* **22**, 443–453. (doi:10.1111/j.1365-2435.2008.01417.x)
 37. Klockmann M, Günter F, Fischer K. 2016 Heat resistance throughout ontogeny: body size constrains thermal tolerance. *Glob. Change Biol.* **23**, 686–696. (doi:10.1111/gcb.13407)
 38. Brylinski JM. 1981 Report on the presence of *Acartia tonsa* Dana (Copepoda) in the harbour of Dunkirk (France) and its geographical distribution in Europe. *J. Plankton Res.* **3**, 255–260. (doi:10.1093/plankt/3.2.255)
 39. Miller CB, Johnson JK, Heinle DR. 1977 Growth rules in the marine copepod genus *Acartia*. *Limnol. Oceanogr.* **22**, 326–335. (doi:10.4319/lo.1977.22.2.0326)
 40. Leandro SM, Tiselius P, Queiroga H. 2006 Growth and development of nauplii and copepodites of the estuarine copepod *Acartia tonsa* from southern Europe (Ria de Aveiro, Portugal) under saturating food conditions. *Mar. Biol.* **150**, 121–129. (doi:10.1007/s00227-006-0336-y)
 41. Di Santo V, Lobel PS. 2017 Body size and thermal tolerance in tropical gobies. *J. Exp. Mar. Biol. Ecol.* **487**, 11–17. (doi:10.1016/j.jembe.2016.11.007)
 42. Geerts AN *et al.* 2015 Rapid evolution of thermal tolerance in the water flea *Daphnia*. *Nat. Clim. Change* **5**, 665–668. (doi:10.1038/ncclimate2628)
 43. Ospina AF, Mora C. 2004 Effect of body size on reef fish tolerance to extreme low and high temperatures. *Environ. Biol. Fish.* **70**, 339–343. (doi:10.1023/B:EBFI.0000035429.39129.34)
 44. Kiørboe T. 2007 Mate finding, mating, and population dynamics in a planktonic copepod *Oithona davisae*: there are too few males. *Limnol. Oceanogr.* **52**, 1511–1522. (doi:10.4319/lo.2007.52.4.1511)
 45. Berggreen U, Hansen B, Kiørboe T. 1988 Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. *Mar. Biol.* **99**, 341–352. (doi:10.1007/BF02112126)
 46. Heinle DR. 1966 Production of a calanoid copepod, *Acartia tonsa*, in the Patuxent River estuary. *Chesapeake Sci.* **7**, 59–74. (doi:10.2307/1351126)
 47. Horne CR, Hirst AG, Atkinson D, Neves A, Kiørboe T. 2016 A global synthesis of seasonal temperature-size responses in copepods. *Global Ecol. Biogeogr.* **25**, 988–999. (doi:10.1111/geb.12460)
 48. Horne CR, Hirst AG, Atkinson D. 2015 Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. *Ecol. Lett.* **18**, 327–335. (doi:10.1111/ele.12413)
 49. Durbin EG, Durbin AG, Smayda TJ, Verity PG. 1983 Food limitation of production by adult *Acartia tonsa* in Narragansett Bay, Rhode Island. *Limnol. Oceanogr.* **28**, 1199–1213. (doi:10.4319/lo.1983.28.6.1199)
 50. Lee RF, Hagen W, Kattner G. 2006 Lipid storage in marine zooplankton. *Mar. Ecol. Prog. Ser.* **307**, 273–306. (doi:10.1016/j.mbs.2006.09.005)
 51. Dam HG, Baumann H. 2017. Climate change, zooplankton and fisheries. In *Climate change impacts on fisheries and aquaculture* (eds BF Phillips, M Pérez-Ramírez). Hoboken, NJ: John Wiley & Sons.
 52. Hoffmann AA, Sgro CM. 2011 Climate change and evolutionary adaptation. *Nature* **470**, 479–485. (doi:10.1038/nature09670)
 53. Barret RDH, Schluter D. 2007 Adaptation from standing genetic variation. *Trends Ecol. Evol.* **23**, 38–44. (doi:10.1016/j.tree.2007.09.008)
 54. Hedrick PW. 2007 Sex: differences in mutation, recombination, selection, gene flow, and genetic drift. *Evol.: Int. J. Org. Evol.* **61**, 2750–2771. (doi:10.1111/j.1558-5646.2007.00250.x)
 55. NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. 2014 Sea-viewing Wide Field-of-view Sensor (SeaWiFS) ocean color data. NASA OB.DAAC, Greenbelt, MD, USA. (doi:10.5067/ORBVIEW-2/SEAWIFS_OC.2014.0)
 56. O'Donnell J, Dam HG, Bohlen WF, Fitzgerald W, Gay PS, Houk AE, Cohen DC, Howard-Strobel MM. 2008 Intermittent ventilation in the hypoxic zone of western Long Island Sound during the summer of 2004. *J. Geophys. Res.: Oceans* **113**, C09025. (doi:10.1029/2007JC004716)

57. R Core Team. 2016 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>
58. Maly EJ, Maly MP. 1998 Body size and sexual size dimorphism in calanoid copepods. *Hydrobiologia* **391**, 173–179. (doi:10.1023/A:1003597614322)
59. Gilbert JJ, Williamson CE. 1983 Sexual dimorphism in zooplankton (Copepoda, Cladocera, and Rotifera). *Annu. Rev. Ecol. Syst.* **14**, 1–33. (doi:10.1146/annurev.es.14.110183.000245)
60. Kearney M, Shine R, Porter WP. 2009 The potential for behavioral thermoregulation to buffer 'cold-blooded' animals against climate warming. *Proc. Natl Acad. Sci. USA* **106**, 3835–3840. (doi:10.1073/pnas.0808913106)
61. Nagelkerken I, Munday PL. 2015 Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community-level responses. *Glob. Change Biol.* **22**, 974–989. (doi:10.1111/gcb.13167)
62. Provan J, Beatty GE, Keating SL, Maggs CA, Savidge G. 2009 High dispersal potential has maintained long-term population stability in the North Atlantic copepod *Calanus finmarchicus*. *Proc. R. Soc. B* **276**, 301–307. (doi:10.1098/rspb.2008.1062)
63. Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M. 2002 Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* **296**, 1692–1694. (doi:10.1126/science.1071329)
64. Gregg WW, Conkright ME, Ginoux P, O'Reilly JE, Casey NW. 2003 Ocean primary production and climate: Global decadal changes. *Geophys. Res. Lett.* **30**, 1219–1214. (doi:10.1029/2003GL016889)
65. Dutkiewicz S, Hickman AE, Jahn O, Henson S, Deaulieu C, Monier E. 2019 Ocean colour signature of climate change. *Nat. Commun.* **10**, 1–13. (doi:10.1038/s41467-019-08457-x)
66. Brown CJ *et al.* 2010 Effects of climate-driven primary production change on marine food webs: implications for fisheries and conservation. *Glob. Change Biol.* **16**, 1194–1212. (doi:10.1111/j.1365-2486.2009.02046.x)
67. Allan BJM, Domenici P, Munday PL, McCormick MI. 2015 Feeling the heat: the effect of acute temperature changes on predator–prey interactions in coral reef fish. *Conserv. Physiol.* **3**, cov011–8. (doi:10.1093/conphys/cov011)
68. Rall BC, Vucic-Pestic O, Ehnes RB, Emmerson M, Brose U. 2009 Temperature, predator–prey interaction strength and population stability. *Glob. Change Biol.* **16**, 2145–2157. (doi:10.1111/j.1365-2486.2009.02124.x)
69. Broitman BR, Szathmari PL, Mislán KAS, Blanchette CA, Helmuth B. 2009 Predator–prey interactions under climate change: the importance of habitat vs body temperature. *Oikos* **118**, 219–224. (doi:10.1111/j.1600-0706.2008.17075.x)
70. Delaney MP. 2003 Effects of temperature and turbulence on the predator–prey interactions between a heterotrophic flagellate and a marine bacterium. *Microb. Ecol.* **45**, 218–225. (doi:10.1007/s00248-002-1058-4)
71. Brown CJ *et al.* 2016 Ecological and methodological drivers of species' distribution and phenology responses to climate change. *Glob. Change Biol.* **22**, 1548–1560. (doi:10.1111/gcb.13184)
72. Edwards M, Richardson AJ. 2004 Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**, 881–884. (doi:10.1038/nature02808)
73. Nguyen AD. 2017 Effects of desiccation and starvation on thermal tolerance and the heat-shock response in forest ants. *J. Comp. Physiol. B* **187**, 1107–1116. (doi:10.1007/s00360-017-1101-x)
74. Brown RP, Griffin S. 2005 Lower selected body temperatures after food deprivation in the lizard *Anolis carolinensis*. *J. Therm. Biol.* **30**, 79–83. (doi:10.1016/j.jtherbio.2004.07.005)
75. Scharf I, Wexler Y, MacMillan HA, Presman S, Simson E, Rosenstein S. 2016 The negative effect of starvation and the positive effect of mild thermal stress on thermal tolerance of the red flour beetle, *Tribolium castaneum*. *Naturwissenschaften* **103**, 1041–1010. (doi:10.1007/s00114-016-1344-5)
76. Fischer K, Dierks A, Franke K, Geister TL, Liszka M, Winter S, Pflücke C. 2010 Environmental effects on temperature stress resistance in the tropical butterfly *Bicyclus anynana*. *PLoS ONE* **5**, e15284-12 (doi:10.1371/journal.pone.0015284)