LIMNOLOGY AND OCEANOGRAPHY
Letters

ASLO
Open Access

Limnology and Oceanography Letters 4, 2019, 53–61

doi: 10.1002/lol2.10106

LETTER

Copepod respiration increases by 7% per °C increase in temperature: A meta-analysis

Kyle B. Heine [1]* *Ash Abebe* [2] *Alan E. Wilson* [3] *Wendy R. Hood* [1]

[1]Department of Biological Sciences, Auburn University, Auburn, Alabama; [2]Department of Mathematics and Statistics, Auburn University, Auburn, Alabama; [3]School of Fisheries, Aquaculture, and Aquatic Sciences, Auburn University, Auburn, Alabama

Scientific Significance Statement

In copepod physiological research, much attention is given to the positive, exponential change in mean respiration rate that occurs with increasing temperature. However, the average rate of change (slope) in respiration rates across more than two temperatures, and whether these rates of change are significant (non-zero), remains to be adequately characterized. This study establishes that copepod respiration rates increase significantly with increasing temperature by approximately 7% per °C, suggesting that copepod respiration is plastic and responsive to increasing water temperatures.

Abstract

Exponential increase in respiration rate with increasing temperature in poikilotherms is well documented, however, the rate of change varies greatly across copepod taxa. Studies often report magnitude of change, but the rate of change in respiration across multiple temperatures is equivocal. We used 32 studies spanning 78 yrs of research and 50 copepod species (three orders) to quantify percent change in respiration rates per one-unit change in temperature. We found that copepod respiration rates increased by approximately 7% per °C increase in water temperature across the orders Calanoida, Cyclopoida, and Harpacticoida. Neither food availability nor scaling respiration to copepod dry weight affected the rate of change of respiration rates. Studies using Winkler titration to measure oxygen consumption produced significantly larger percent changes in respiration, whereas newer methods such as fiber optics produced smaller effects. These results have far reaching implications for understanding how copepod respiration responds to increasing water temperatures.

The rate of chemical reactions is generally known to increase with increasing temperature (Arrhenius law). Thus, studies focused on physiological adaptation commonly evaluate changes in metabolism with changes in thermal environments. More than 90 studies have evaluated the relation between temperature and respiration in copepods, with most either measuring temperature and respiration rates concurrently to evaluate the mechanisms that underlie environmental adaptation (e.g., Anraku 1964; Auel et al. 2005) or evaluate individual responses to acclimation treatments (e.g., Pascal

*Correspondence: kbh0039@tigermail.auburn.edu

Author Contribution Statement: K.B.H. and W.R.H. conceived the study. K.B.H., A.A., and A.E.W. collected the data. K.B.H. analyzed the data. All authors contributed to writing the manuscript.

Data availability statement: Data and metadata are available at https://doi.org/10.5061/dryad.jk353fs.

Additional Supporting Information may be found in the online version of this article.

and Chong 2016; Liu and Ban 2017). Yet, despite the large number of experimental and observational measurements, we have a limited understanding of how the energetic demands of copepods respond to increasing temperature.

Respiration rates of animals are influenced by several intrinsic and extrinsic variables, including temperature, body size, and food availability (Nakamura and Turner 1997; Ikeda et al. 2001; Ikeda et al. 2007; Pedersen et al. 2014; Morata and Søreide 2015). The speed by which substrates interact with enzymes in the mitochondrial matrix and electron transport system increases with increasing temperature (Packard et al. 1971; Bode et al. 2013) due to the chemical nature of respiratory processes that use oxygen to produce ATP, carbon dioxide, and water. This can be seen experimentally when copepods are acclimated to different temperatures in the lab (e.g., Raymont 1959; Pascal and Chong 2016; Liu and Ban 2017), as well as when respiration is measured in both warm and cold temperatures in the field (e.g., Li et al. 2004; Teuber et al. 2013; Cass and Daly 2014). Given the vital role of oxygen in the respiratory process, it is important to understand the environmental and intrinsic factors that influence rate of oxygen consumption in key primary consumers such as copepods.

Larger organisms exhibit higher respiration rates due to the greater energetic demand of maintaining more tissue but lower respiration rates per unit mass (Bode et al. 2013). Differences in size and respiration rate may also be tied to sex and age in species with sexual dimorphism and indeterminate growth (Weymouth et al. 1944; Fenchel 1974). Additionally, food intake provides substrate for oxidative phosphorylation. Thus, the availability of phytoplankton will influence the ability of copepods to sustain respiration (Cruz et al. 2013). Such studies examine the magnitude (mean values) of respiration rates between select temperatures; however, the rate (slope) by which copepods accomplish this increase in respiration across multiple temperatures is more obscure (Supporting Information Fig. S1).

The effect of temperature on respiration is often examined by calculating Q_{10} values (e.g., Gaudy et al. 2000; Kiko et al. 2016). Q_{10} measurements are typically based on change in the rate of reaction or respiration at two temperatures. The limited scope of these measurements limits an investigator's ability to accurately extrapolate changes in respiration beyond two temperatures. Thus, measuring percent change in respiration rate (rate $\cdot$ $^{\circ}C^{-1}$) across numerous points on a log-linear scale should provide a more accurate prediction (*see* "Effect size: percent change in respiration" for an explanation of rate calculation in exponential and log-linear models).

The aim of this study was to explain how copepod respiration (dissolved oxygen) may respond to warming waters as a result of climate change. We asked the specific question: how much do copepod respiration rates change with a degree change in water temperature for calanoid, cyclopoid, and harpacticoid copepods? We also examined the effect of fasting on copepod respiration rates. To determine if copepod respiration rates increase significantly with temperature, we conducted a formal, random-effects meta-analysis without moderators. The method used to measure dissolved oxygen, food availability, and whether or not studies scaled respiration rates by copepod dry weight (DW) were included as categorical moderators in meta-analytical mixed-effects models to further delineate heterogeneity in respiration. If copepod respiration rates display a plastic response to water temperature, we expect the rate of change in respiration rates to increase significantly (a non-zero increase) with increasing temperature. We also expect studies that fed copepods prior to respiration measurements to display higher rates of change in oxygen consumption with increasing temperature in comparison to studies that fasted copepods.

Methods

Literature search

Following the Preferred Reporting Items of Systematic reviews and Meta-Analyses (PRISMA) recommendations (Moher et al. 2009), we used two databases to quantify respiration rates across a range of temperatures for three orders of copepods while controlling for the method used to measure dissolved oxygen, food availability, and the incorporation of DW into respiration measurements. We searched Google Scholar and Web of Science using the search term "copepod respiration" from 02 to 13 February 2018. Most studies were not useful; therefore, we refined our searches accordingly. We used the search criteria "in title" to search Google Scholar, returning 47 articles (10 collected); "all topics" was used to search Web of Science, returning 407 articles (72 collected). Both databases were also searched using "copepod oxygen" on 17 February 2018. We used "in title" to search both databases, returning 38 articles for Google Scholar (three collected) and 39 for Web of Science (one collected). We also searched the literature cited of acquired articles for appropriate studies (five collected).

To be included in our analyses, each study must have reported—at a minimum—organismal oxygen consumption across two or more temperatures. We excluded studies that reported respiration rates at only one temperature or across temperatures with a range not greater than 1°C. We did not include review papers, but acquired appropriate papers from reviews to directly calculate effect sizes. The search criteria yielded an initial collection of 86 articles, of which we screened based on the following criteria (Supporting Information Fig. S2).

Studies that reported mean oxygen consumption across an uncertain range of temperatures (e.g., 1–5°C) were excluded. Suboptimal or exceedingly high temperatures known to denature or damage proteins (Somero 1995) were excluded from our calculations. We also excluded studies that failed to report the number of replicates per mean value.

We only included studies that measured oxygen consumption at the organismal level and not CO_2 production, N consumption, C : O ratios, or oxygen consumption based on electron transport activity. We did not feel that attempts to convert said values to organismal oxygen consumption would be accurate (Glazier 2005). Studies that measured oxygen consumption per unit of DW were coded separately from those that did not incorporate DW.

Effect size estimation

Given the rate of change in oxygen consumption across temperatures is often identical between sexes, only differing in magnitude (Weymouth et al. 1944; Isla and Perissinotto 2004; Liu and Ban 2017), we combined male and female data and reported the life history stage of individuals (i.e., nauplius, copepodid, and adult), in addition to whether studies included DW if applicable, to control for size. Individual data points of different life history stages in comparison to the rest of the study were removed when calculating effect sizes to accurately represent body size.

We reported the family and order of copepods to account for phylogenetic non-independence. Separate effect sizes were calculated for each species where applicable. We also recorded the method used to measure dissolved oxygen. Studies that used polarography to measure oxygen but did not specify using Clark-type electrodes were coded as using "polarographic electrodes."

Both experimental and observational studies were used to be as inclusive as possible.

Data acquisition

We calculated 78 effect sizes from 32 studies from 1939 to 2017, including 50 species from three copepod orders. Several studies reported functions of data graphed with y-axes fit to either $\log_{10}$, ln, or exponential scaling; for these studies, we extracted data from graphs using ImageJ (Schindelin et al. 2012) and transformed the measured values to the original data using $(10^Y) \cdot 100^{-1}$ for ln graphs and $(10^Y) \cdot 10^{-1}$ for $\log_{10}$ graphs. These values, and measures taken directly from exponential graphs, were transformed to natural log values to acquire variance estimates. Our line estimate of $\log_{10}$ respiration differed from that reported in McAllen et al. (1999), although our graph coincided with that of the study. In this one instance, we used the β_1 estimate of 0.0971 acquired from our extracted data.

Most studies reported mean respiration rates for a given value of temperatures. In these cases, we used the mean, reported error estimate (SD or SE), and n number of replicates per mean to calculate β_1 and the original sampling variance of the raw data (*see* "Effect size: percent change in respiration"). For studies that reported mean values and range (no SD or SE available), we calculated the SD using (range $\cdot 4^{-1}$), assuming a small number of replicates that were normally distributed per mean. If only the range and median using boxplots were reported, we calculated the mean using ((min + 2(median) + max) $\cdot 4^{-1}$), for sample sizes < 25 (Hozo et al. 2005).

Effect size: Percent change in respiration

For each species within each study, we calculated percent change in respiration per one-unit increase in temperature. Given that respiration increases exponentially with temperature, we used β_1 of the exponential function $R = \beta_0 \cdot e^{\beta_1 T}$ to calculate our effect size. Here, β_1 coincides with β_1 of the log-linear respiration model, expressed as $\ln R = \ln\beta_0 + \beta_1 T$. We calculated percent change in respiration as:

$$\%\text{change} = \left(e^{\beta_1} - 1\right) \cdot 100$$

Variance in percent change (V) was calculated using the delta method (Ver Hoef 2012):

$$V = (100)^2 \cdot e^{2\beta_1} \cdot (\text{SE})^2$$

where SE is the standard error of the log-linear respiration model.

For studies that did not report the SE and β_1 of the log-linear or exponential model but only mean values at given temperatures, we calculated the original sampling variance of the log-linear model slope as:

$$\text{SE}^2 = \frac{\left(\sigma_1^2 + \sigma_2^2\right)/\left(\sum n - 2\right)}{\sum\left(n \cdot (x - \bar{x})^2\right)}$$

where σ_1^2 is $\sum((n-1) \cdot \sigma_{\text{LM}}^2)$, σ_2^2 is $\sum(n \cdot (\ln R - \ln f)^2)$, n is a vector containing the number of replicates for each mean at a given temperature x, and $\bar{x}$ is $\sum(n \cdot x)/\sum n$. σ_{LM}^2 is the variance of a given mean ln respiration rate at temperature x, $\ln R$ is the natural log respiration rates, and $\ln f$ is the fitted values of the log-linear model. For studies that reported the standard error of mean rates (σ_{M}), we first calculated σ_{LM} using ($\sigma_{\text{M}} \cdot \text{mean}^{-1}$); this was derived using the delta method (Ver Hoef 2012). This σ_{LM}^2 was then used in the calculation of SE^2.

Random-effects meta-analyses and mixed modeling

Using a Bayesian approach, we conducted formal, random-effects meta-analyses without moderators to quantify percent change in copepod respiration rates per degree change in temperature across calanoid, cyclopoid, and harpacticoid copepod orders and calanoid families. To further examine the heterogeneity in copepod respiration with increasing temperature, we conducted meta-analytical mixed-effects modeling with methodology, food availability, or DW as categorical moderators.

A common concern of meta-analysis is nonindependent effect sizes within and between studies; examples include calculating effect sizes of identical taxa or calculating multiple effect sizes from one study (Nakagawa et al. 2017). We conducted random-effects meta-analyses with authorship and ultrametric phylogenies of either Calanoida families or Calanoida, Cyclopoida, and Harpacticoida orders as random effects. We also included species as a random effect to account

for non-independence when calculating mean effects for each family- or order-level phylogeny. Relatedness of copepod orders was obtained from Khodami et al. (2017), and family-level relatedness was determined from Blanco-Bercial et al. (2010) and Bradford-Grieve et al. (2010). Model prior parameters of $V = 1$ and nu (degree of belief) = 1 were used for all random effects. Model parameters were based on posterior distributions of 5000 samples.

Meta-analytical mixed-effects models included food availability, the method used to measure dissolved oxygen, or whether studies scaled respiration by DW, as categorical moderators; these models also included the random effects listed above. Both newer (fiber optics) and older (Winkler titration) dissolved oxygen measurement methods were included as reference groups. We did not have enough replicates to include life history stage or water salinity as moderators in our analyses, nor examine moderator effects within Harpacticoida or Cyclopoida (*see* Supporting Information Table S3 for variable descriptions). One study did not report the taxon of copepods.

Copepod respiration is known to increase with temperature, however, several of our effect size estimates show negative percent changes in this relationship (i.e., respiration rates decrease as temperature increases). We ran sensitivity analysis by removing these unexpected, negative effects and reanalyzing percent changes at the family level as all negative effect sizes stemmed from Calanoida. To test for publication bias, we qualitatively examined funnel plot asymmetry, as well as a bubble plot of effect sizes plotted against publication year. Funnel plots portray effect size estimates plotted against the standard error of those estimates. Asymmetry in the plot, or estimates that fall outside the confidence intervals, indicate possible publication bias. Bias and overall effect size heterogeneity was assessed by modeling author (categorical) and publication year (continuous) as moderators using Restricted Maximum Likelihood "REML" in "metafor." All phylogenetic meta-analyses were completed using the package "MCMCglmm" (Hadfield 2010; Hadfield and Nakagawa 2010) and "ape" (Paradis et al. 2004) in R version 3.4.4 (R Core Team 2018). We used "ggplot2" (Wickham 2002) and "metafor" (Viechtbauer 2010) for graphical development (Supporting Information Code S4).

Results

Effects of temperature on copepod respiration

Although copepod respiration is known to increase exponentially with temperature, we have yet to determine if the increase is significant (non-zero) and the rate (function slope) of such an increase. While including authorship, order-level phylogeny, and species as random effects, we determined that respiration exhibited a significant, non-zero increase of 7.51% per one-unit increase in temperature (Table 1). Order-level relatedness with corresponding meta-analytical means and 95% credible intervals (CIs) are presented in Fig. 1.

We included authorship, family-level phylogeny, and species as random effects in our analysis of calanoid copepods and found that respiration increased by 6.67% per one-unit increase in temperature (Table 1). Family-level relatedness with corresponding meta-analytical means and 95% CIs are presented in Fig. 2. Effects with 95% CIs that do not overlap zero are considered statistically significant ($\alpha = 0.05$).

Methodology, food availability, and DW

Upon further examining the heterogeneity in respiration, we found that the method used to measure dissolved oxygen significantly influenced effect size estimates across all three orders of copepods. Both newer (fiber optics) and older (gas chromatography) methods produced significantly smaller percent changes in respiration when compared to the commonly used Winkler titration method. We also found that Winkler titration produced significantly larger percent changes in respiration with increasing temperature than polarographic electrodes (Table 1). In other words, copepod respiration increased at a significantly higher rate with temperature as measured by Winkler titration.

Fiber optic meters are becoming increasingly popular in respiration research, nevertheless, Clark-type electrodes are used routinely. Effect size estimates using fiber optics did not differ significantly from those obtained using Clark-type electrodes, nor from older methods such as Cartesian divers or manometers (Table 1). We did not have enough replicates to assess the impact of methodology at the family level.

Provided that food intake supplies a greater amount of available substrate for oxidative phosphorylation, we hypothesized that the respiration rates of copepods fed prior to respiration measurements would increase at a higher rate in response to increasing temperature than copepods that were fasted. However, the presence of food did not affect the manner in which respiration responded to increasing temperature in the order- or family-level models (Table 1).

Lastly, several studies have scaled respiration by copepod DW to account for greater respiration rates of larger copepods. We found no difference between effect size estimates that did or did not scale respiration by DW (Table 1).

Sensitivity analysis

Given the positive relationship between respiration and temperature, not including exceedingly high or low temperatures, we did not anticipate finding negative percent changes in the literature. Therefore, we ran sensitivity analysis at the family level by removing all negative effects from our model. This provides a further understanding of how studies that calculated decreases in respiration with increasing temperature influenced our results. With family-level phylogeny, authorship, and species as random effects, we found that respiration increased by 7.97% with increasing temperature (l-CI 95% = 6.01, u-CI 95% = 9.96, $p < 0.001$).

Table 1. Results of random-effects meta-analyses and mixed-effects models of Calanoida, Cyclopoida, and Harpacticoida orders and Calanoida families including DW, food availability, and methodology modeled as categorical moderators. Author, family/order-level phylogeny, and species were included as random effects in all models. *n* represents the number of effect sizes. Significant *p* values are in bold.

Level	Model	*n*	Mean (% change)	Lower CI (95%)	Upper CI (95%)	*p*
Order	**Random effects**	77	7.51	4.59	10.80	**<0.01**
	DW					
	Included[1]	42	−0.13	−2.46	2.23	0.91
	Food					
	Starved[2]	61	−1.06	−6.79	4.11	0.69
	Method[3]					
	Cartesian diver	4	−2.45	−10.70	5.20	0.55
	Clark-type	16	−1.29	−4.64	1.89	0.42
	Fiber optics	24	−4.36	−8.14	−0.62	**<0.05**
	Gas chromatography	10	−6.01	−12.10	−0.28	**<0.05**
	Manometer	5	−4.57	−9.26	0.64	0.06
	Polarography	2	−9.02	−14.29	−4.55	**<0.001**
	Method[4]					
	Cartesian diver	4	1.91	−6.67	9.77	0.63
	Clark-type	16	3.07	−0.60	6.58	0.09
	Gas chromatography	10	−1.65	−7.49	4.37	0.57
	Manometer	5	−0.23	−5.56	5.20	0.94
	Polarography	2	−4.71	−9.78	0.42	0.07
	Winkler titration	16	4.30	0.58	8.12	**<0.05**
Family	**Random effects**	68	6.67	3.81	9.37	**<0.01**
	DW					
	Included[1]	38	−0.48	−2.97	2.09	0.70
	Food					
	Starved[2]	58	−2.06	−9.95	5.30	0.57

[1]In comparison to DW excluded in study measurements.
[2]In comparison to copepods fed during study measurements.
[3]Winkler titration as reference level.
[4]Fiber optics as reference level.

Publication bias

We qualitatively analyzed funnel plot asymmetry of effect sizes and standard error and found that several effect sizes fell outside the 95% and 99% confidence intervals (Fig. 3). We also examined publication bias as a function of publication year using a bubble plot (Supporting Information Fig. S5). Several negative effects were deemed outliers, confirming our decision to remove these values in our sensitivity analysis. We found no significant effect of authorship or publication year on effect size estimates ($p > 0.05$). Heterogeneity between study effect sizes was estimated at $I^2 = 96.9\%$.

Discussion

The rate of increase of copepod respiration across a broad range of temperatures varies greatly among published studies. We calculated percent change in respiration rates across 32 studies (Supporting Information S6) and addressed the question: how much do copepod respiration rates change with a degree change in water temperature for calanoid, cyclopoid, and harpacticoid copepods? Respiration rate increased by 7.51% among these three orders, and 6.67% within Calanoida. However, when negative effects were removed from our family-level model, percent change in Calanoida respiration increased from 6.67% to 7.97%.

Commonly used Q_{10} values limit an investigator's capacity to predict copepod respiration rates across a broad range of temperatures because Q_{10} values are based on two temperatures. Furthermore, Q_{10} values must be interpreted through comparison to other Q_{10} values. The effect size of 7% reported here demonstrates how respiration rates change across the full range of published temperatures across which copepods are viable. Because these equations are based on many temperatures, we believe that percent change is more accurate in predicting respiration rates than Q_{10}.

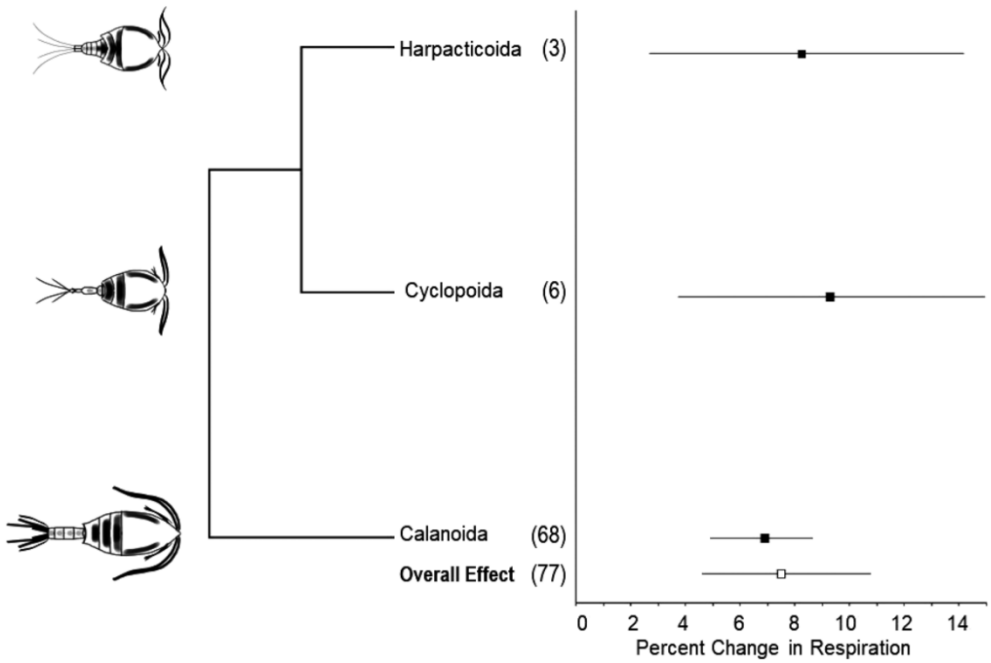

Fig. 1. Meta-analytical, mean percent changes in respiration with 95% CIs of Calanoida, Cyclopoida, and Harpacticoida copepod orders. Overall effect represents the collective effect of all three orders. Number of effect sizes per order is in parentheses. Effect size estimates with CIs that do not overlap zero are considered statistically significant (α = 0.05).

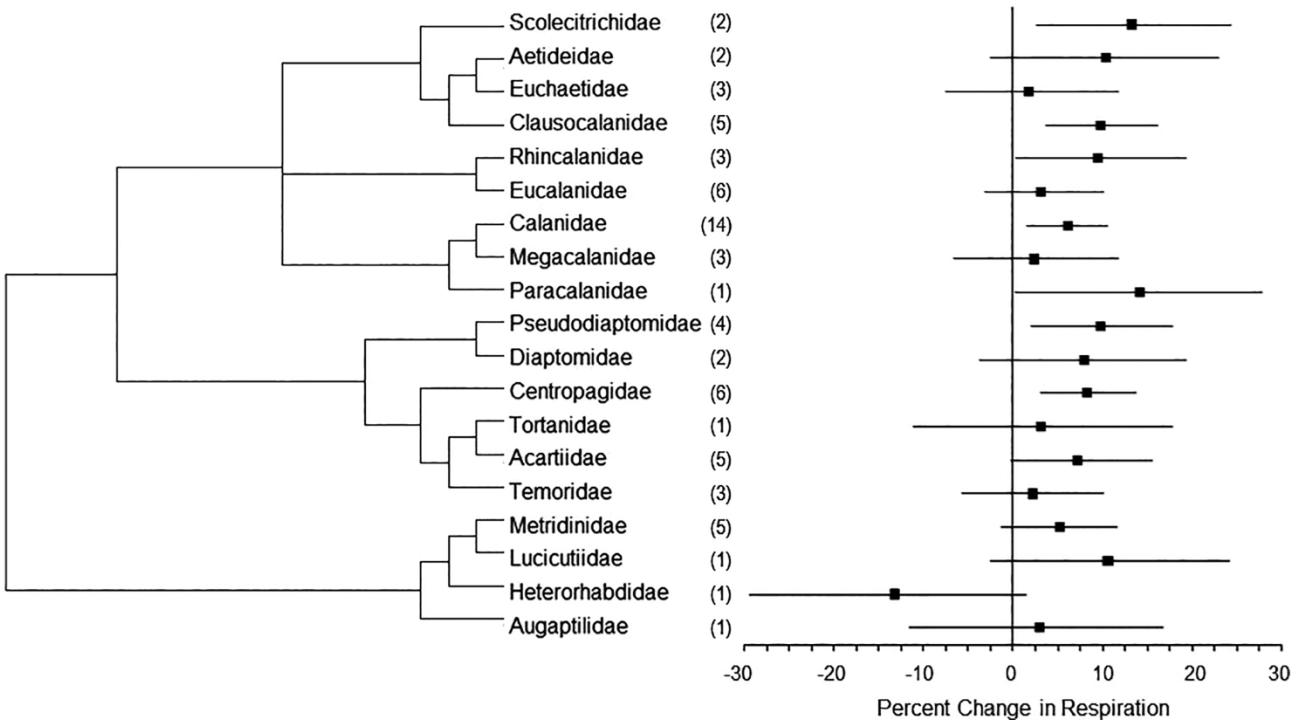

Fig. 2. Meta-analytical, mean percent changes in respiration with 95% CIs of Calanoida copepod families. Number of effect sizes per family is in parentheses. Effect size estimates with CIs that do not overlap zero are considered statistically significant (α = 0.05).

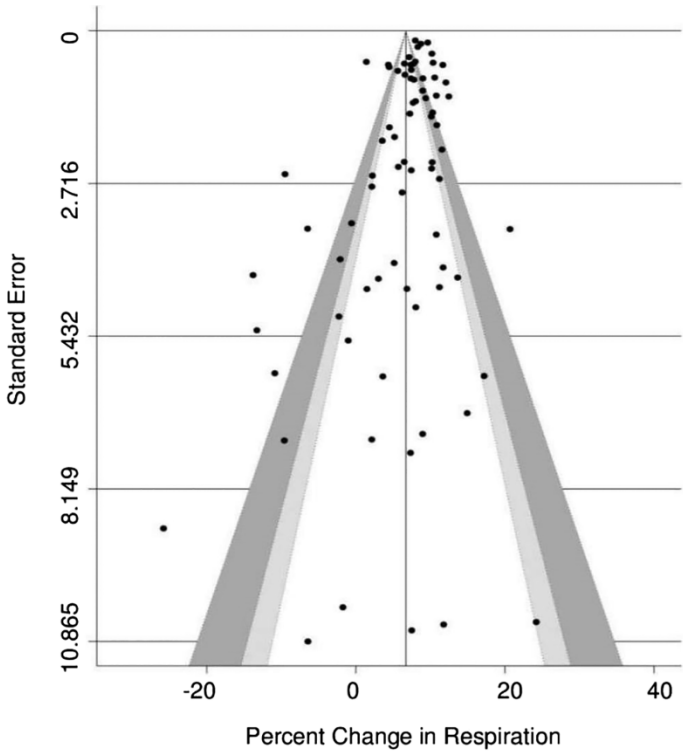

Fig. 3. Funnel plot of effect sizes plotted against standard error to assess asymmetry and publication bias. Point estimates that display asymmetry in the plot or fall outside the confidence intervals indicate possible publication bias. White, light gray, and dark gray shading correspond to 90%, 95%, and 99% confidence intervals.

We examined the effect of fasting on copepod respiration rates and hypothesized that percent change in respiration of fed copepods would be greater than fasted copepods. We found no support for this hypothesis. This result does not imply that the respiration rates of fed copepods are similar to starved copepods, but concludes that food availability does not affect how copepod respiration responds to increasing temperature. Although larger organisms exhibit higher organismal respiration rates on average than smaller organisms (Bode et al. 2013), copepod studies have been inconsistent in their decision to scale respiration measurements to copepod DW. Given this dichotomy in study design, we compared effect sizes between these studies but found no significant difference in percent change in respiration.

Recent technological advances, such as fiber optics, allow researchers to measure respiration non-invasively without consuming oxygen in the process (Preininger et al. 1994). We compared effect sizes across studies that used recent advances (fiber optics) with older methods that are still in use (Winkler titration). Winkler titration produced significantly larger percent changes in respiration with increasing temperature than fiber optics, gas chromatography, and polarography.

Several inquiries have been conducted regarding the accuracy of Winkler titration and optical oxygen sensors. Optical oxygen sensors are largely variable in their response time—influenced by stirring—and therefore, membrane thickness and material should be selected carefully in accordance with stirring (Markfort and Hondzo 2009). This contrasts with possible inaccuracies of Winkler titration, including the oxygen contribution of reagents (Carpenter 1965). Provided that Winkler titration has a greater accuracy (Markfort and Hondzo 2009) and is used to calibrate other oxygen sensors, future research needs to further develop the accuracy and response time of non-Winkler methods as a function of increasing temperature.

Percent change in respiration of 6% to 7% corroborates the results of Green (1975), Teare and Price (1979), Gaudy et al. (2000), Li et al. (2015), Kiko et al. (2016), and Svetlichny et al. (2017). However, studies such as Isla and Perissinotto (2004), Castellani et al. (2005), and Teuber et al. (2013) reported increasingly large changes in respiration with increasing temperature, whereas Raymont (1959) and Castellani and Altunbaş (2014) reported exceedingly small or negative relationships (Raymont 1959; Ikeda 1979; Teuber et al. 2013). Although investigators may not expect respiration to decrease with increasing temperature, it is important that researchers discuss these relationships to determine why studies measure such trends (e.g., taxonomic relatedness).

Organisms respond in vastly different ways to increasing water temperature; therefore, it is important to understand the physiological responses of organisms including primary consumers such as copepods. Previous studies have demonstrated that certain species of *Calanus* and *Oithona*, for example, withstand a relatively large increase in water temperature from −1.7°C to 8°C from June to July during seasonal vertical migrations (Darnis and Fortier 2014). Our study elaborates on such findings by characterizing the ability of copepods to increase their respiration rates in response to increasing water temperature. We conclude that copepod respiration rates increase significantly with temperature (a non-zero increase) by 7% per °C. This result is a crucial first step in understanding the physiological response of copepods to increasing water temperature; however, the effects of other environmental factors such as ocean acidification (Vehmma et al. 2013) and increasing CO_2 (Runge et al. 2016) warrant further investigation.

References

Anraku, M. 1964. Influence of the Cape Cod Canal on the hydrography and on the copepods in Buzzards Bay and Cape Cod Bay, Massachusetts. II. Respiration and feeding. Limnol. Oceanogr. **2**: 195–206. doi:10.4319/lo.1964.9.2.0195

Auel, H., W. Hagen, W. Ekau, and H. M. Verheye. 2005. Metabolic adaptations and reduced respiration of the copepod *Calanoides carinatus* during diapause at depth in the Angola-Benguela front and northern Benguela upwelling regions. Afr. J. Mar. Sci. **27**: 653–657. doi:10.2989/18142320509504125

Blanco-Bercial, L., J. Bradford-Grieve, and A. Bucklin. 2010. Molecular phylogeny of the Calanoida (Crustacea: Copepoda). Mol. Phylogenet. Evol. **1**: 103–113. doi:10.1016/j.ympev.2011.01.008

Bode, M., A. Schukat, W. Hagen, and H. Auel. 2013. Predicting metabolic rates of calanoid copepods. J. Exp. Mar. Biol. Ecol. **444**: 1–7. doi:10.1016/j.jembe.2013.03.003

Bradford-Grieve, J. M., G. A. Boxshall, S. T. Ahyong, and S. Ohtsuka. 2010. Cladistic analysis of the calanoid Copepoda. Invertebr. Syst. **24**: 291–321. doi:10.1071/IS10007

Carpenter, J. H. 1965. The accuracy of the Winkler method for dissolved oxygen analysis. Limnol. Oceanogr. **10**: 135–140. doi:10.4319/lo.1965.10.1.0135

Cass, C. J., and K. L. Daly. 2014. Eucalanoid copepod metabolic rates in the oxygen minimum zone of the eastern tropical North Pacific: Effects of oxygen and temperature. Deep-Sea Res. Part I Oceanogr. Res. Pap. **94**: 137–149. doi:10.1016/j.dsr.2014.09.003

Castellani, C., C. Robinson, T. Smith, and R. S. Lampitt. 2005. Temperature affects respiration rate of *Oithona similis*. Mar. Ecol. Prog. Ser. **285**: 129–135. doi:10.3354/meps285129

Castellani, C., and Y. Altunbaş. 2014. Seasonal change in acclimatised respiration rate of *Temora longicornis*. Mar. Ecol. Prog. Ser. **500**: 83–101. doi:10.3354/meps10661

Cruz, J., S. Garrido, M. S. Pimentel, R. Rosa, A. M. Santos, and P. Ré. 2013. Reproduction and respiration of a climate change indicator species: Effect of temperature and variable food in the copepod *Centropages chierchiae*. J. Plankton Res. **35**: 1046–1058. doi:10.1093/plankt/fbt057

Darnis, G., and L. Fortier. 2014. Temperature, food and the seasonal vertical migration of key arctic copepods in the thermally stratified Amundsen Gulf (Beaufort Sea, Arctic Ocean). J. Plankton Res. **36**: 1092–1108. doi:10.1093/plankt/fbu035

Fenchel, T. 1974. Intrinsic rate of natural increase: The relationship with body size. Oecologia **14**: 317–326. doi:10.1007/BF00384576

Gaudy, R., G. Cervetto, and M. Pagano. 2000. Comparison of the metabolism of *Acartia clausi* and *A. tonsa*: Influence of temperature and salinity. J. Exp. Mar. Biol. Ecol. **247**: 51–65. doi:10.1016/S0022-0981(00)00139-8

Glazier, D. S. 2005. Beyond the '3/4-power law': Variation in the intra-and interspecific scaling of metabolic rate in animals. Biol. Rev. Camb. Philos. Soc. **4**: 611–662. doi:10.1017/S1464793105006834

Green, J. D. 1975. Feeding and respiration in the New Zealand copepod *Calamoecia lucasi* Brady. Oecologia **21**: 345–358. doi:10.1007/BF00345826

Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. J. Stat. Softw. **33**: 1–22. doi:10.18637/jss.v033.i02

Hadfield, J. D., and S. Nakagawa. 2010. General quantitative genetic methods for comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical characters. J. Evol. Biol. **23**: 494–508. doi:10.1111/j.1420-9101.2009.01915.x

Hozo, S. P., B. Djulbegovic, and I. Hozo. 2005. Estimating the mean and variance from the median, range, and the size of a sample. BMC Med. Res. Methodol. **5**: 13. doi:10.1186/1471-2288-5-13

Ikeda, T. 1979. Respiration rates of copepod larvae and a ciliate from a tropical sea. J. Oceanogr. Soc. Japan **35**: 1–8. doi:10.1007/BF02108277

Ikeda, T., Y. Kanno, K. Ozaki, and A. Shinada. 2001. Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. Mar. Biol. **139**: 587–596. doi:10.1007/s002270100608

Ikeda, T., F. Sano, and A. Yamaguchi. 2007. Respiration in marine pelagic copepods: A global-bathymetric model. Mar. Ecol. Prog. Ser. **339**: 215–219. doi:10.3354/meps339215

Isla, J. A., and R. Perissinotto. 2004. Effects of temperature, salinity and sex on the basal metabolic rate of the estuarine copepod *Pseudodiaptomus hessei*. J. Plankton Res. **5**: 579–583. doi:10.1093/plankt/fbh049

Khodami, S., J. V. McArthur, L. Blanco-Bercial, and P. M. Arbizu. 2017. Molecular phylogeny and revision of copepod orders (Crustacea: Copepoda). Sci. Rep. **7**: 9164. doi:10.1038/s41598-017-06656-4

Kiko, R., H. Hauss, F. Buchholz, and F. Melzner. 2016. Ammonium excretion and oxygen respiration of tropical copepods and euphausiids exposed to oxygen minimum zone conditions. Biogeosciences **13**: 2241–2255. doi:10.5194/bg-13-2241-2016

Li, C., S. Sun, R. Wang, and X. Wang. 2004. Feeding and respiration rates of a planktonic copepod (*Calanus sinicus*) oversummering in Yellow Sea cold bottom waters. Mar. Biol. **145**: 149–157. doi:10.1007/s00227-004-1306-x

Li, W., G. Han, Y. Dong, A. Ishimatsu, B. D. Russell, and K. Gao. 2015. Combined effects of short-term ocean acidification and heat shock in a benthic copepod *Tigriopus japonicus* Mori. Mar. Biol. **162**: 1901–1912. doi:10.1007/s00227-015-2722-9

Liu, X., and S. Ban. 2017. Effects of acclimatization on metabolic plasticity of *Eodiaptomus japonicus* (Copepoda: Calanoida) determined using an optical oxygen meter. J. Plankton Res. **39**: 111–121. doi:10.1093/plankt/fbw084

Markfort, C. D., and M. Hondzo. 2009. Dissolved oxygen measurements in aquatic environments: The effects of changing temperature and pressure on three sensor technologies. J. Environ. Qual. **38**: 1766–1774. doi:10.2134/jeq2008.0197

McAllen, R., A. C. Taylor, and J. Davenport. 1999. The effects of temperature and oxygen partial pressure on the rate of oxygen consumption of the high-shore rock pool copepod *Tigriopus brevicornis*. Comp. Biochem. Physiol. Part A Mol. Integr. Physiol. **123**: 195–202. doi:10.1016/S1095-6433(99)00050-1

Moher, D., A. Liberati, J. Tetzlaff, D. G. Altman, and The PRISMA Group. 2009. Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. PLoS Med. **6**: e1000097. doi:10.1371/journal.pmed.1000097

Morata, N., and J. E. Søreide. 2015. Effect of light and food on the metabolism of the Arctic copepod *Calanus glacialis*. Polar. Biol. **38**: 67–73. doi:10.1007/s00300-013-1417-2

Nakagawa, S., D. W. Noble, A. M. Senior, and M. Lagisz. 2017. Meta-evaluation of meta-analysis: Ten appraisal questions for biologists. BMC Biol. **15**: 18. doi:10.1186/s12915-017-0357-7

Nakamura, Y., and J. T. Turner. 1997. Predation and respiration by the small cyclopoid copepod *Oithona similis*: How important is feeding on ciliates and heterotrophic flagellates? J. Plankton Res. **19**: 1275–1288. doi:10.1093/plankt/19.9.1275

Packard, T. T., M. L. Healy, and F. A. Richards. 1971. Vertical distribution of the activity of the respiratory electron transport system in marine plankton. Limnol. Oceanogr. **1**: 60–70. doi:10.4319/lo.1971.16.1.0060

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of phylogenetics and evolution in R language. Bioinformatics **20**: 289–290. doi:10.1093/bioinformatics/btg412

Pascal, L., and V. C. Chong. 2016. Does developmental temperature modulate copepods respiratory activity through adult life? J. Plankton Res. **38**: 1215–1224. doi:10.1093/plankt/fbw058

Pedersen, S. A., O. J. Håkedal, I. Salaberria, A. Tagliati, L. M. Gustavson, B. M. Jenssen, A. J. Olsen, and D. Altin. 2014. Multigenerational exposure to ocean acidification during food limitation reveals consequences for copepod scope for growth and vital rates. Environ. Sci. Technol. **48**: 12275–12284. doi:10.1021/es501581j

Preininger, C., I. Klimant, and O. S. Wolfbeis. 1994. Optical fiber sensor for biological oxygen demand. Anal. Chem. **66**: 1841–1846. doi:10.1021/ac00083a011

R Core Team. 2018, *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, [accessed 2018 August 18]. Available from https://www.R-project.org/

Raymont, J. E. 1959. The respiration of some planktonic copepods. Limnol. Oceanogr. **4**: 479–491. doi:10.4319/lo.1959.4.4.0479

Runge, J. A., D. M. Fields, C. R. Thompson, S. D. Shema, R. M. Bjelland, C. M. Durif, A. B. Skiftesvik, and H. I. Browman. 2016. End of the century CO_2 concentrations do not have a negative effect on vital rates of *Calanus finmarchicus*, an ecologically critical planktonic species in North Atlantic ecosystems. ICES J. Mar. Sci. **73**: 937–950. doi:10.1093/icesjms/fsv258

Schindelin, J., and others. 2012. Fiji: An open-source platform for biological-image analysis. Nat. Methods **9**: 676–682. doi:10.1038/nmeth.2019

Somero, G. N. 1995. Proteins and temperature. Annu. Rev. Physiol. **57**: 43–68. doi:10.1146/annurev.ph.57.030195.000355

Svetlichny, L., E. Hubareva, and M. Isinibilir. 2017. Comparative trends in respiration rates, sinking and swimming speeds of copepods *Pseudocalanus elongatus* and *Acartia clausi* with comments on the cost of brooding strategy. J. Exp. Mar. Biol. Ecol. **488**: 24–31. doi:10.1016/j.jembe.2016.12.005

Teare, M., and R. Price. 1979. Respiration of the meiobenthic harpacticoid copepod, *Tachidius discipes* Giesbrecht, from an estuarine mudflat. J. Exp. Mar. Biol. Ecol. **41**: 1–8. doi:10.1016/0022-0981(79)90077-7

Teuber, L., R. Kiko, F. Séguin, and H. Auel. 2013. Respiration rates of tropical Atlantic copepods in relation to the oxygen minimum zone. J. Exp. Mar. Biol. Ecol. **448**: 28–36. doi:10.1016/j.jembe.2013.06.012

Vehmma, A., H. Hogfors, E. Gorokhova, A. Brutemark, T. Holmborn, and J. Engström-Öst. 2013. Projected marine climate change: Effects on copepod oxidative status and reproduction. Ecol. Evol. **3**: 4548–4557. doi:10.1002/ece3.839

Ver Hoef, J. M. 2012. Who invented the delta method? Am. Stat. **66**: 124–127. doi:10.1080/00031305.2012.687494

Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. J. Stat. Softw. **3**: 1–48. doi:10.18637/jss.v036.i03

Weymouth, F. W., J. M. Crismon, V. E. Hall, H. S. Belding, and J. Field. 1944. Total and tissue respiration in relation to body weight a comparison of the kelp crab with other crustaceans and with mammals. Physiol. Zool. **17**: 50–71. doi:10.1086/physzool.17.1.30151829

Wickham, H. 2002, *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. doi:10.1111/j.1467-985X.2010.00676_9.x

Acknowledgments

Special thanks to Nathan Hall and Nicholas M. Justyn for assistance with R coding. We also thank the Hill and Hood labs for comments on the original manuscript and two anonymous reviewers for their comments in review. This project was supported, in part, by the Alabama Agricultural Experiment Station and the Hatch Program of the U.S. Department of Agriculture, National Institute of Food and Agriculture.

Submitted 08 September 2018
Revised 04 March 2019
Accepted 11 March 2019