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

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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% / ^{o}C, suggesting that copepod respiration is plastic and responsive to increasing water temperatures.

Data Availability Statement:
Data and metadata are available at [insert URL].

Abstract:
Exponential increase in respiration rate with increasing temperature in poikilotherms is well documented, however, the overall 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 years of research and 50 copepod species (three orders) to quantify percent increase in respiration rates per one-unit increase in temperature. We found that copepod respiration rates increased by approximately 7% per one ^{o}C increase in water temperature across three well-studied 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 understating how copepod respiration responds to increasing water temperatures.

Keywords:
copepod, exponential function, meta-analysis, percent change, respiration, temperature

Introduction

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 80 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 (Anraku 1964; Auel et al. 2005) or evaluate individual responses to acclimation treatments (Pascal 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 (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 (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

84 (slope) by which copepods accomplish this increase in respiration across multiple
85 temperatures is more obscure (Fig. S1 in the supplement).
86 The effect of temperature on respiration is often examined by calculating Q_{10}
87 values (Gaudy et al. 2000; Kiko et al. 2016). Q_{10} measurements are typically based on
88 change in the rate of reaction or respiration at two temperatures. The limited scope of
89 these measurements limits an investigator's ability to accurately extrapolate changes in
90 respiration beyond two temperatures. Thus, measuring percent change in respiration
91 rate (rate $\cdot$ $°C^{-1}$) across numerous points on a log-linear scale should provide a more
92 accurate prediction (see 'Effect size: percent change in respiration' for an explanation of
93 rate calculation in exponential and log-linear models).
94 The aim of this study was to explain how copepod respiration (dissolved oxygen)
95 may respond to warming waters as a result of climate change. We asked the specific
96 question: how much do copepod respiration rates increase with a degree change in
97 water temperature for calanoid, cyclopoid, and harpacticoid copepods? We also
98 examined the effect of fasting on copepod respiration rates. To determine if copepod
99 respiration rates increase significantly with temperature, we conducted a formal,
100 random-effects meta-analysis without moderators. Study methodology, food availability,
101 and whether or not studies scaled respiration rates by copepod dry weight (DW), were
102 included as categorical moderators in meta-analytical mixed-effects models to further
103 delineate heterogeneity in respiration. If copepod respiration rates display a plastic
104 response to water temperature, we expect the rate of change in respiration rates to
105 increase significantly (a non-zero increase) with increasing temperature. We also expect
106 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 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 methodological approach, 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 February 2 - February 13, 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 February 17, 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 minimum—organismal oxygen consumption across two or more temperatures. 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 (Diagram S2 in the Supplement):

We used studies that reported oxygen consumption across more than one value of temperature. We excluded studies that reported respiration rates at only one

temperature or across temperatures with a range not greater than 1°C. 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 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, adult), in addition to whether studies included DW if applicable, to control for size. Single data points of a different life history stage 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 respiration. Studies that

used polarography to measure respiration 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 $(\text{range} \cdot 4^{-1})$, 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 $((\text{min} + 2(\text{median}) + \text{max}) \cdot 4^{-1})$, 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:

$$\% \text{ change} = (e^{\beta 1} - 1) \cdot 100.$$

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

$$V = (100)^2 \cdot e^{2\beta 1} \cdot (SE)^2,$$

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:

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

where σ_1^2 is $\sum ((n - 1) \cdot \sigma_{LM}^2)$, 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 ($\sigma_M \cdot \text{mean}^{-1}$); 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 non-independent 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 priors of V = 1 and nu = 1 were used for all random effects. Model parameters were based on posterior distributions of 5,000 samples.

Meta-analytical mixed-effects models included food availability, the methodology used to measure respiration, 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 Table S3 in the supplement 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 re-analyzing percent changes at the family level since 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 '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 (Code S4 in the Supplement).

Results

Effects of temperature on 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 credible intervals are presented in Figure 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 credible intervals are presented in Figure 2. Effects with 95% credible intervals (CIs) that do not overlap zero are considered statistically significant (α = 0.05).

Study methodology, food availability, and dry weight

Upon further examining the heterogeneity in respiration, we found that the methodology used to measure respiration 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 did fiber optics differ 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 in 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, $p < 0.001$).

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 effect size bias as a function of publication year using a bubble plot (Fig. S5 in the supplement). 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 $I^2 = 96.93\%$.

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 (S6 in the Supplement) and addressed the question: how much do copepod respiration rates increase 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}.

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 more 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.

335 Percent change in respiration of 6 to 7% corroborates the results of Green
336 (1975), Teare and Price (1979), Gaudy et al. (2000), Li et al. (2015), Kiko et al. (2016),
337 and Svetlichny (2017). However, studies such as Isla and Perissinotto (2004),
338 Castellani et al. (2005), and Teuber et al. (2013) reported increasingly large changes in
339 respiration with increasing temperature, whereas Raymont (1959) and Castellani and
340 Altunbas (2014) reported exceedingly small or negative relationships (Raymont 1959;
341 Ikeda 1979; Teuber et al. 2013). Although investigators may not expect respiration to
342 decrease with increasing temperature, it is important that researchers discuss these
343 relationships to determine why studies measure such trends (e.g., taxonomic
344 relatedness).
345 Organisms respond in vastly different ways to increasing water temperature,
346 therefore, it is important to understand the physiological responses of organisms
347 including primary consumers such as copepods. Previous studies have demonstrated
348 that certain species of *Calanus* and *Oithona*, for example, withstand a relatively large
349 increase in water temperature from -1.7 to 8°C from June to July during seasonal
350 vertical migrations (Darnis and Fortier 2014). Our study elaborates on such findings by
351 characterizing the ability of copepods to increase their respiration rates in response to
352 increasing water temperature. We conclude that copepod respiration rates increase
353 significantly with temperature (a non-zero increase) by 7% / °C. This result is a crucial
354 first step in understanding the physiological response of copepods to increasing water
355 temperature, however, the effects of other environmental factors such as ocean
356 acidification (Vehmma et al. 2013) and increasing CO_2 (Runge et al. 2016) warrant
357 further investigation.

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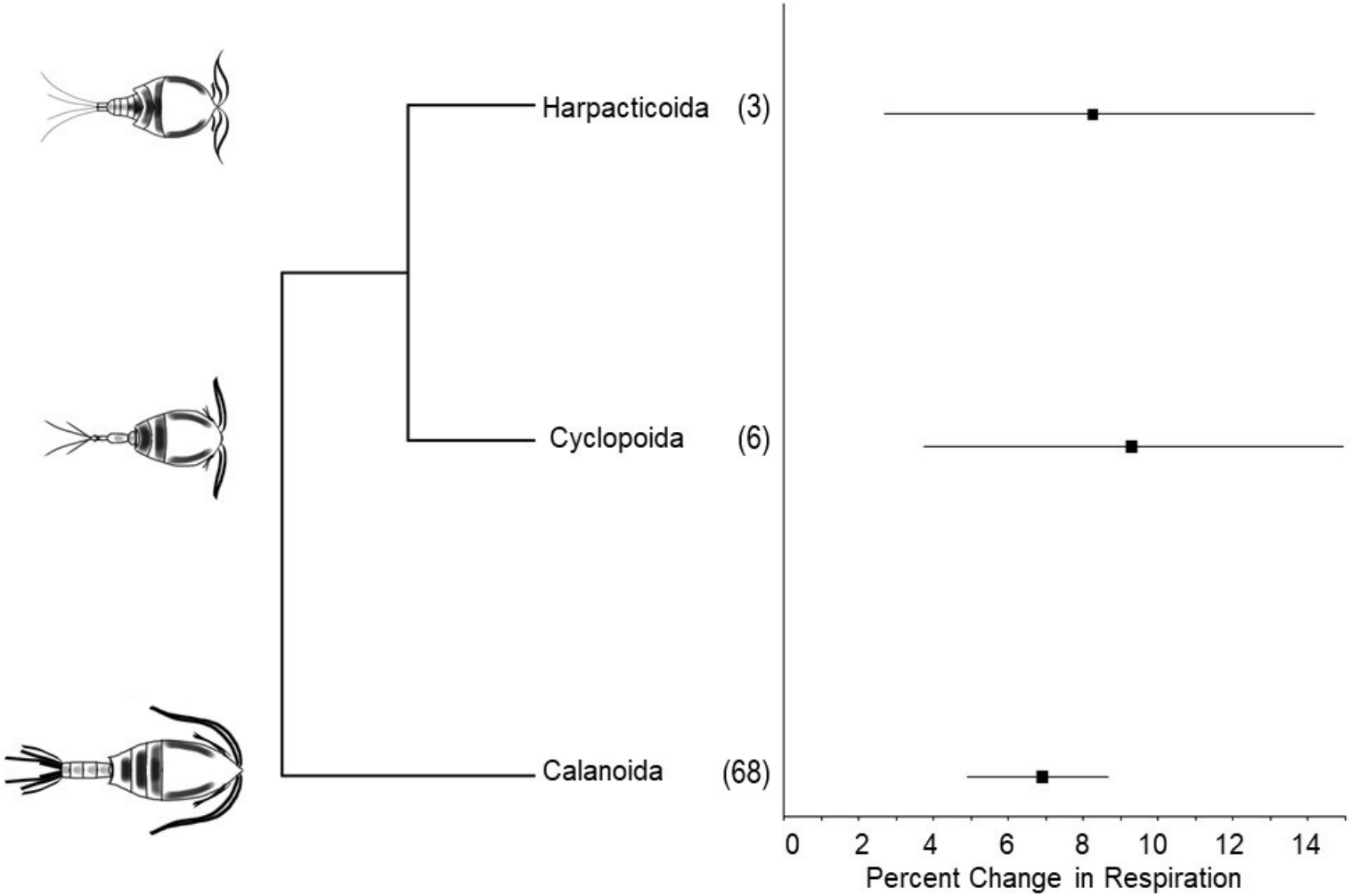
Table 1. Results of random-effects meta-analyses and mixed-effects models of Calanoida, Cyclopoida, and Harpacticoida orders and Calanoida families including dry weight (DW), food availability, and methodology modeled as categorical moderators. Author, family/order-level phylogeny, and species were included as random effects in all models. n represents the number of effect sizes. Significant p-values are in bold. [a]In comparison to DW excluded in study measurements. [b]In comparison to copepods fed during study measurements. [c]Winkler titration as reference level. [d]Fiber optics as reference level.

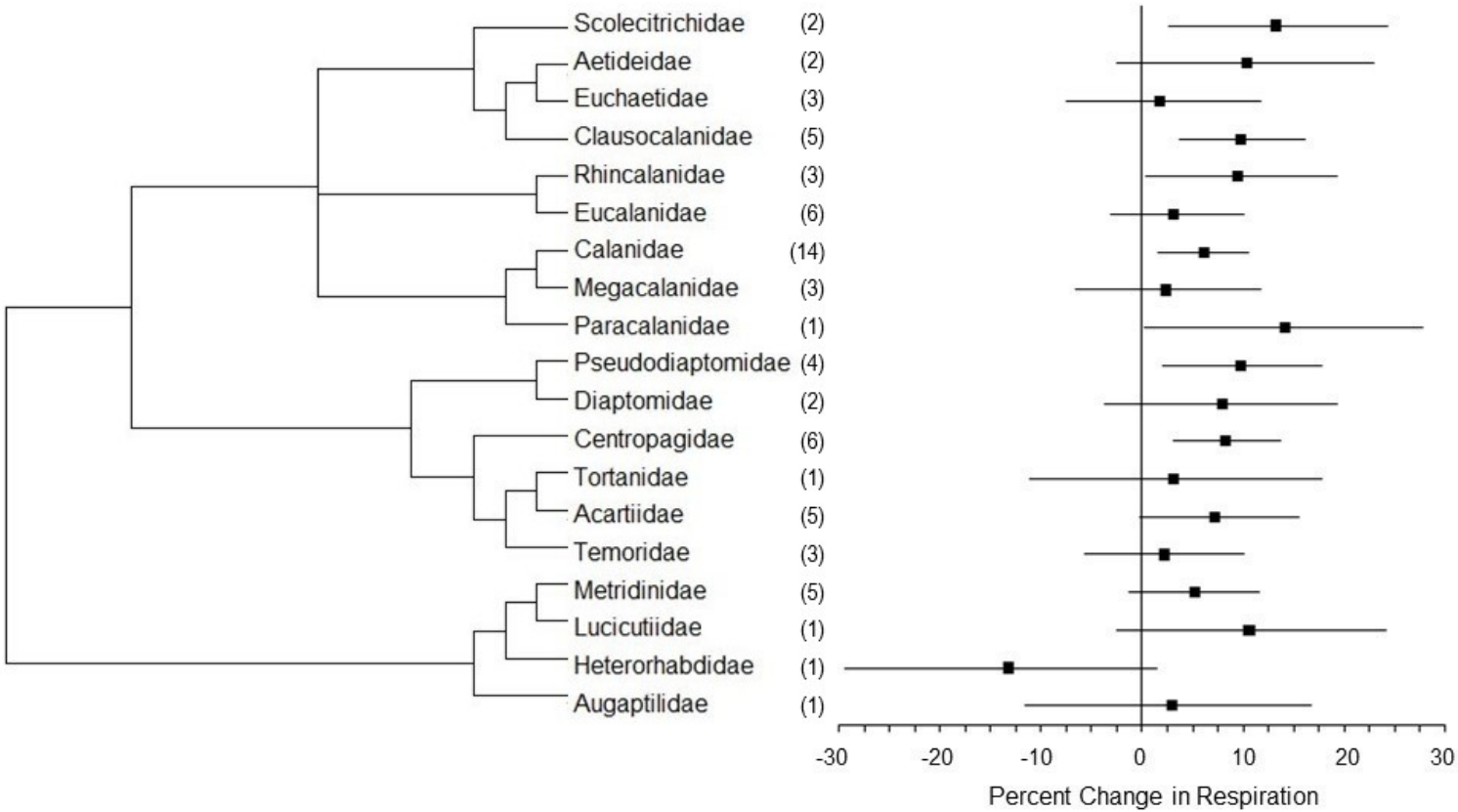
Level	Model	n	Mean (% Change)	Lower CI (95%)	Upper CI (95%)	p
Order	**Random effects**	77	7.51	4.59	10.80	**< 0.01**
	~ DW					
	Included[a]	42	-0.13	-2.46	2.23	0.91
	~ Food					
	Starved[b]	61	-1.06	-6.79	4.11	0.69
	~ Method[c]					
	Cartesian diver	4	-2.45	-10.70	5.20	0.55
	Clark-type	16	-1.29	-4.64	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[d]					
	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[a]	38	-0.48	-2.97	2.09	0.70
	~ Food					
	Starved[b]	58	-2.06	-9.95	5.30	0.57

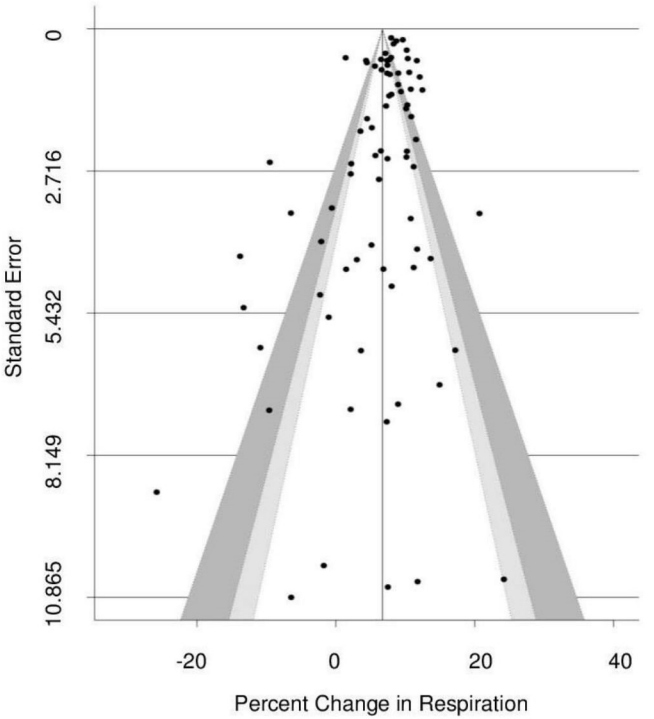
Fig. 1. Meta-analytical, mean percent changes in respiration with 95% credible intervals of Calanoida, Cyclopoida, and Harpacticoida copepod orders. Number of effect sizes per order is in parentheses. Effect size estimates with credible intervals that do not overlap zero are considered statistically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

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

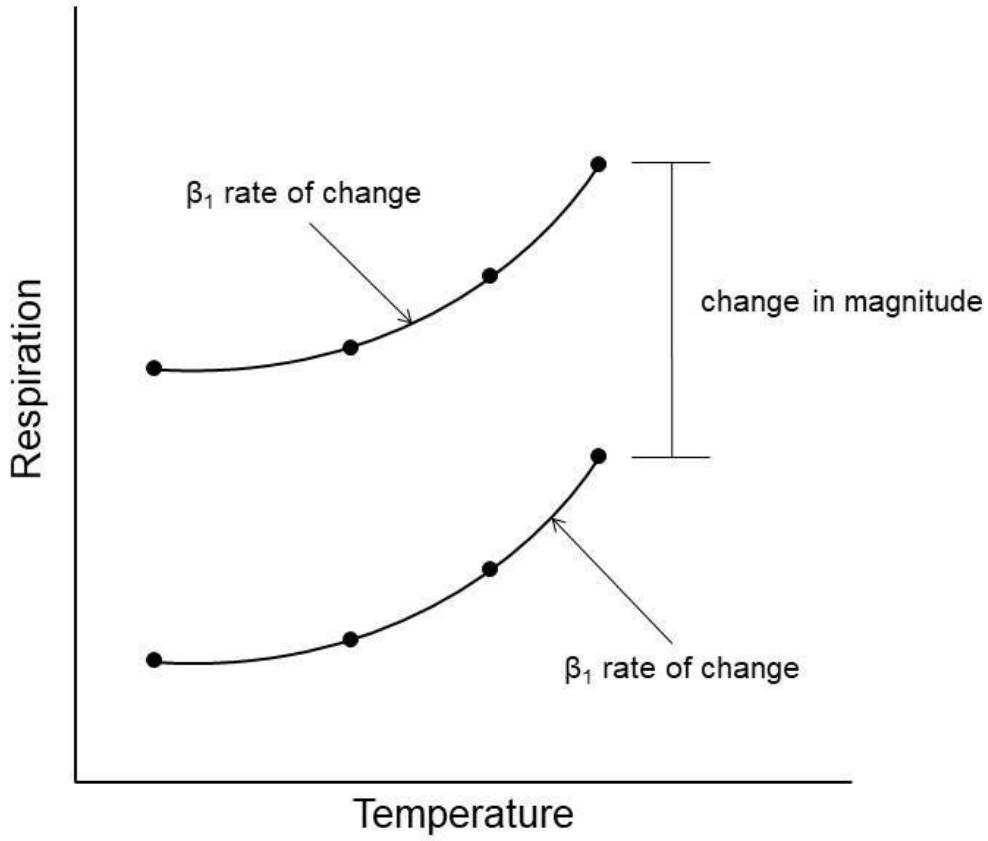
Fig. 3. Funnel plot of effect sizes plotted against standard error to assess asymmetry and publication bias. Point estimates that display asymmetry in the plot or fall outside the confidence intervals indicate possible publication bias. White, light gray, and dark gray shading correspond to 90, 95, and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


Harpacticoida
(3)
Cyclopoida
(6)
Calanoida
(68)
0
2
4
6
8
10
12
14
Percent Change in Respiration

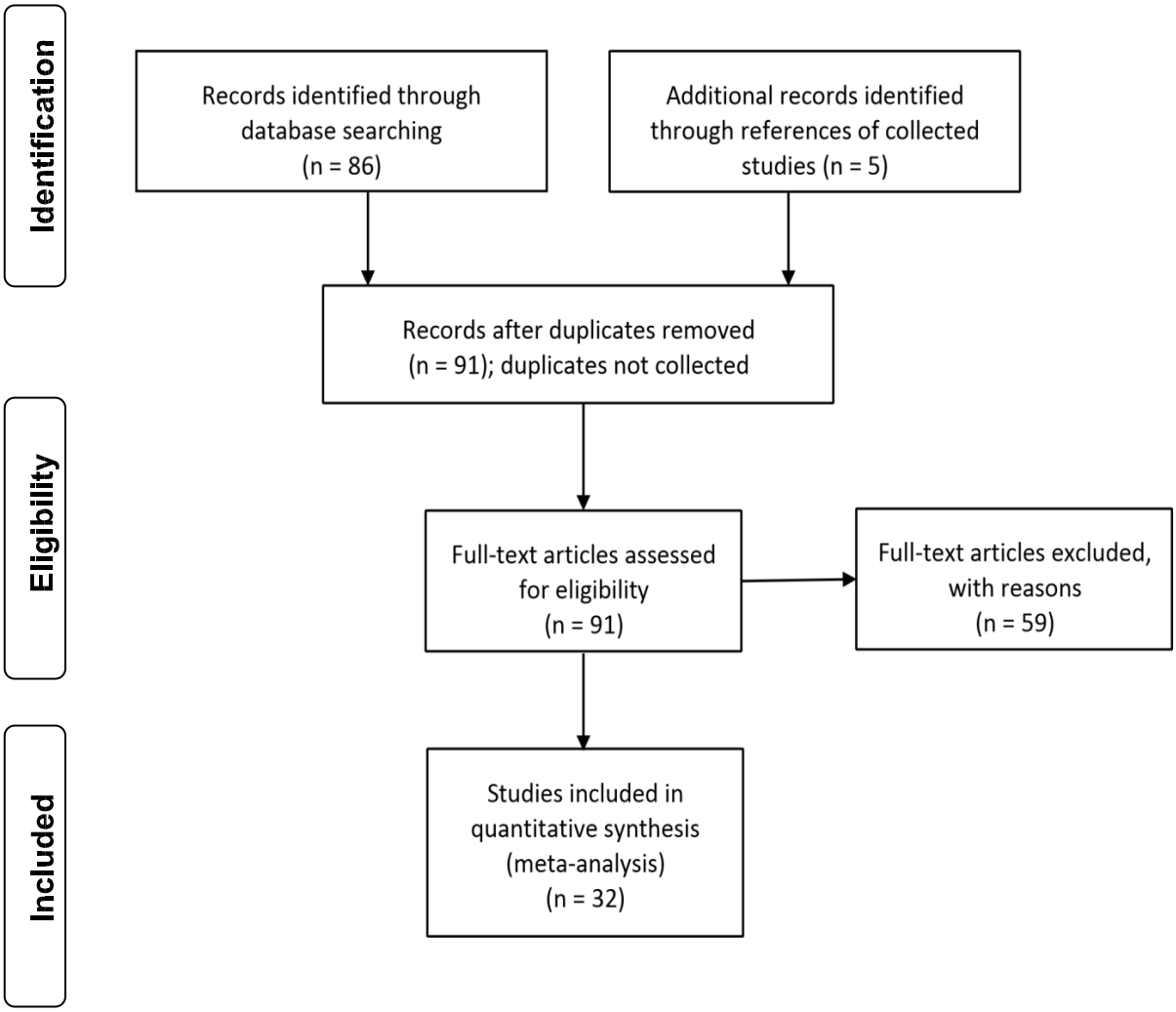

Scolecitrichidae (2)
Aetideidae (2)
Euchaetidae (3)
Clausocalanidae (5)
Rhincalanidae (3)
Eucalanidae (6)
Calanidae (14)
Megacalanidae (3)
Paracalanidae (1)
Pseudodiaptomidae (4)
Diaptomidae (2)
Centropagidae (6)
Tortanidae (1)
Acartiidae (5)
Temoridae (3)
Metridinidae (5)
Lucicutiidae (1)
Heterorhabdidae (1)
Augaptilidae (1)
-30
-20
-10
0
10
20
30
Percent Change in Respiration


Standard Error
0
2.716
5.432
8.149
10.865
-20
0
20
40
Percent Change in Respiration

S1 Figure demonstrating the change in magnitude between respiration at each temperature versus β_1 used in our study to calculate percent change, irrespective of changing magnitude. Our study does not assess differences in mean respiration rates at select temperatures as indicated by the change in magnitude, but assesses differences in the rate of change in respiration rates with increasing temperature (slope) as indicated by the β_1 rate of change.



S2 Flow diagram of study identification, eligibility screening, and inclusion.



S3 Table summary of variables included in meta-analytical models and how each was coded, as well as the levels within each variable if applicable.

Variable	Coded	Levels
Dry weight	Factor	Yes, No
Family, Order	Factor	*Taxon*, *Taxon*
Food	Factor	Fed, Starved
Lead author	Factor	*Name*
Method	Factor	Cartesian diver, Clark-type electrode, fiber optic meter, gas chromatography, manometer, polarographic electrode, Winkler titration
Percent change	Numeric	*Continuous*
Publication year	Numeric	*Continuous*
Species	Factor	*Taxon*
Variance	Numeric	*Continuous*

S4 R code.

```
### Calculate original sampling variance of the log-linear model slope
### for studies that reported means at temps x, n number of replicates
### per mean, and error variance for each mean

p.var1 <- sum((n-1)*var)
yhats <- lm(lnY~x)$fitted.values
p.var2 <- sum(n*(lnY - yhats)^2)
numerator <- (p.var1 + p.var2)/(sum(n) - 2)
x.mean <- sum(n*x)/sum(n)
denominator <- sum(n*(x - x.mean)^2)
numerator/denominator


### Calculate percent change and variances for loglinear models; for
### studies reporting mean values, the above calculation was used in
### place of ll.se^2 in the code below

### Input: predictor (x) and log response (lnY)
### Output: effect size (% change in response per unit change in x),
### variance of the effect, and sample size

ll.reg <- lm(lnY ~ x)
ll.sum <- summary(ll.reg)
ll.slope <- ll.sum$coefficients[2,1]
ll.se <- ll.sum$coefficients[2,2]
ll.effect <- 100*(exp(ll.slope) - 1)
ll.var <- 10000*exp(2*ll.slope)*(ll.se^2)
ans <- cbind(ll.effect, ll.var, length(lnY))
colnames(ans) <- paste(c("Effect Size", "Variance", "n"))
rownames(ans) <- paste("")
print(round(ans,4))



########## Phylogenetic meta-analysis of copepod orders ##########

### Clean working environment
rm(list=ls())

### Load required packages
library(MCMCglmm)
library(ape)
library(phytools)

### Set working directory
setwd("C:/Users/Kyle/Desktop/Meta/Meta-ana")

### Read in and attach data
d<-read.table("Meta_Data_No_Food.txt",header=T)
attach(d)

### Create and attach tree of copepod orders
tree <-'(Calanoida,(Cyclopoida,Harpacticoida));'
tree <- read.newick(text=tree)
attach(tree)
```

```
### Make tree ultrametric and plot it
tree <- compute.brlen(tree, method="Grafen")
is.ultrametric(tree)
plot(tree)

### Match tips to data
check.species<-function(x) {any(x==tree$tip.label)}
print(check.species)

### Apply above function and remove missing data; data file is a copy
### of the original data but without food to prevent unnecessary deletion of
### rows with NAs using the following.
d <- d[sapply(d[,"Order"],check.species),]

### Return complete columns
d <-  d[complete.cases(d),]
print(head(d))

### Invert phylogenetic covariance matrix
INtree <- inverseA(tree, nodes="ALL")

### Set priors
prior <- list(R=list(V=1, nu=0.002),
G=list(G1=list(V=1, nu=1),
                      G2=list(V=1, nu=1),G3=list(V=1, nu=1)))

### Run model without moderators
model.Order <- MCMCglmm(Change ~ 1,
random= ~ Order + Author + Species,
data=d, ginverse=list(Order = INtree$Ainv),
mev=d$Variance,
prior=prior,
nitt=1000000,
thin=100,
burnin=500000)

summary(model.Order)

 Iterations = 500001:999901
 Thinning interval  = 100
 Sample size  = 5000

 DIC: -90.81881

 G-structure:  ~Order
       post.mean l-95% CI u-95% CI eff.samp
Order     4.998  0.07086    13.49     5000

               ~Author

       post.mean l-95% CI u-95% CI eff.samp Author
7.155    1.842    14.68     4612

               ~Species
         post.mean l-95% CI u-95% CI
eff.samp Species     16.57    5.942    29.16
5227

 R-structure:  ~units
```

```
      post.mean  l-95% CI u-95% CI eff.samp units
0.4285 0.0001596    2.187     2229

 Location effects: Change ~ 1

            post.mean l-95% CI u-95% CI eff.samp  pMCMC
(Intercept)     7.511    4.596   10.802     3775 0.0036 ** ---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1



### Effect of dry weight on effect size estimates (order level)
model.DryWeight <- MCMCglmm(Change ~ DW,
random = ~ Order + Author + Species,
data = d, ginverse = list(Order = INtree$Ainv),
mev = d$Variance,
prior = prior,
nitt = 1000000,
thin = 100,
burnin = 500000)

summary(model.DryWeight)

 Iterations = 500001:999901
 Thinning interval  = 100
 Sample size  = 5000

 DIC: -95.78628

 G-structure:  ~Order
       post.mean l-95% CI u-95% CI eff.samp
Order     4.132  0.07023    13.74     5000

               ~Author
        post.mean l-95% CI u-95% CI
eff.samp Author     7.362    1.806    15.04
4210

               ~Species
         post.mean l-95% CI u-95% CI
eff.samp Species     16.86    5.304    29.32
5000

 R-structure:  ~units

      post.mean l-95% CI u-95% CI eff.samp units
0.4316 0.000117    2.121     2285

 Location effects: Change ~ DW
             post.mean l-95% CI u-95% CI eff.samp  pMCMC
(Intercept)    7.5724   4.2174  11.0539     5000 0.0052 **
DWyes         -0.1364  -2.4622   2.2338     5000 0.9144    ---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1



### Effect of methodology (Winkler_titration as reference; order level)
model.Method1 <- MCMCglmm(Change ~ relevel(Method, ref="Winkler_titration"),
random = ~ Order + Author + Species,
```

```
data = d, ginverse = list(Order = INtree$Ainv),
mev = d$Variance,
prior = prior,
nitt = 1000000,
thin = 100,
burnin = 500000)

summary(model.Method1)

 Iterations = 500001:999901
 Thinning interval  = 100
 Sample size  = 5000

 DIC: -80.231

 G-structure:  ~Order
       post.mean l-95% CI u-95% CI eff.samp
Order     4.346  0.08372    14.15     5000

              ~Author
        post.mean l-95% CI u-95% CI eff.samp
Author     3.729   0.1685     8.27     4262

              ~Species
         post.mean l-95% CI u-95% CI
eff.samp Species     15.07    5.283    26.14
5000

 R-structure:  ~units
       post.mean  l-95% CI u-95% CI eff.samp
units    0.3984 0.0001467     2.04     2489

 Location effects: Change ~ relevel(Method, ref = "Winkler_titration")
                                                                post.mean l-95% CI
(Intercept)                                                      10.1464   6.5397
relevel(Method, ref = "Winkler_titration")Cartesian_diver         -2.4520 -10.7071
relevel(Method, ref = "Winkler_titration")Clark_type_electrode    -1.2903  -4.6469
relevel(Method, ref = "Winkler_titration")fiber_optic_meter       -4.3614  -8.1449
relevel(Method, ref = "Winkler_titration")gas_chromatography      -6.0188 -12.1041
relevel(Method, ref = "Winkler_titration")manometer               -4.5784  -9.2696
relevel(Method, ref = "Winkler_titration")polarographic_electrode  -9.0264 -14.2936

                                                                u-95% CI eff.samp  pMCMC
(Intercept)                                                     14.0160     5000 0.0020
relevel(Method, ref = "Winkler_titration")Cartesian_diver         5.2045     5415 0.5512
relevel(Method, ref = "Winkler_titration")Clark_type_electrode    1.8971     5000 0.4240
relevel(Method, ref = "Winkler_titration")fiber_optic_meter      -0.6204     5000 0.0272
relevel(Method, ref = "Winkler_titration")gas_chromatography     -0.2840     4955 0.0444
relevel(Method, ref = "Winkler_titration")manometer               0.6486     5000 0.0628
relevel(Method, ref = "Winkler_titration")polarographic_electrode -4.5573     4778 <2e-04
                                                                   (Intercept)
**  relevel(Method, ref = "Winkler_titration")Cartesian_diver
relevel(Method, ref = "Winkler_titration")Clark_type_electrode       relevel(Method,
ref = "Winkler_titration")fiber_optic_meter       *   relevel(Method, ref =
"Winkler_titration")gas_chromatography      *   relevel(Method, ref =
"Winkler_titration")manometer               .   relevel(Method, ref =
"Winkler_titration")polarographic_electrode *** ---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
### Effect of methodology (fiber_optic_meter as reference; order level)
model.Method2 <- MCMCglmm(Change ~ relevel(Method, ref="fiber_optic_meter"),
random = ~ Order + Author + Species,data = d,
ginverse = list(Order = INtree$Ainv),
mev = d$Variance,
prior = prior,
nitt = 1000000,
thin = 100,
burnin = 500000)

summary(model.Method2)

 Iterations = 500001:999901
 Thinning interval  = 100
 Sample size  = 5000

 DIC: -82.01482

 G-structure:  ~Order
       post.mean l-95% CI u-95% CI eff.samp
Order     4.583  0.05296    12.26     5000

              ~Author
        post.mean l-95% CI u-95% CI eff.samp
Author      3.74   0.1689    8.073     4782

              ~Species
         post.mean l-95% CI u-95% CI
eff.samp Species     15.18    5.557    26.68
5000

 R-structure:  ~units

      post.mean  l-95% CI u-95% CI eff.samp units
0.3864 0.0001589    2.022     2462

 Location effects: Change ~ relevel(Method, ref = "fiber_optic_meter")
                                                                 post.mean l-95% CI
(Intercept)                                                        5.8099   2.2270
relevel(Method, ref = "fiber_optic_meter")Cartesian_diver          1.9166  -6.6744
relevel(Method, ref = "fiber_optic_meter")Clark_type_electrode     3.0766  -0.6097
relevel(Method, ref = "fiber_optic_meter")gas_chromatography      -1.6538  -7.4955
relevel(Method, ref = "fiber_optic_meter")manometer               -0.2387  -5.5679
relevel(Method, ref = "fiber_optic_meter")polarographic_electrode -4.7129  -9.7891
relevel(Method, ref = "fiber_optic_meter")Winkler_titration         4.3038   0.5880

                                                                 u-95% CI eff.samp
pMCMC (Intercept)                                                   9.9416     5090
0.0072 relevel(Method, ref = "fiber_optic_meter")Cartesian_diver                9.7780
5000 0.6324 relevel(Method, ref = "fiber_optic_meter")Clark_type_electrode     6.5804
5000 0.0960 relevel(Method, ref = "fiber_optic_meter")gas_chromatography        4.3764
5000 0.5796 relevel(Method, ref = "fiber_optic_meter")manometer                 5.2005
5000 0.9484 relevel(Method, ref = "fiber_optic_meter")polarographic_electrode   0.4236
5000 0.0740 relevel(Method, ref = "fiber_optic_meter")Winkler_titration         8.1272
5000 0.0292
                                                                   (Intercept)
** relevel(Method, ref = "fiber_optic_meter")Cartesian_diver
relevel(Method, ref = "fiber_optic_meter")Clark_type_electrode   .  relevel(Method,
ref = "fiber_optic_meter")gas_chromatography         relevel(Method, ref =
"fiber_optic_meter")manometer                  relevel(Method, ref =
```

```
"fiber_optic_meter")polarographic_electrode .  relevel(Method, ref =
"fiber_optic_meter")Winkler_titration       *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1



### Calculate meta-analytical means of each order; saved as separate file
### Set priors
prior2 <- list(R=list(V=1, nu=0.002),
G=list(G1=list(V=1, nu=1),
                      G2=list(V=1, nu=1)))

model.Order.Fixed <- MCMCglmm(Change ~ Order - 1,
random= ~ Author + Species,
data=d, ginverse=list(Order = INtree$Ainv),
mev=d$Variance,
prior=prior2,
nitt=1000000,
thin=100,
burnin=500000)

summary(model.Order.Fixed)

 Iterations = 500001:999901
 Thinning interval  = 100
 Sample size  = 5000

 DIC: -93.72902

 G-structure:  ~Author

       post.mean l-95% CI u-95% CI eff.samp Author
7.146    1.824     14.3     5000

               ~Species

        post.mean l-95% CI u-95% CI eff.samp Species
17.65    6.703    31.38     5327

 R-structure:  ~units
       post.mean  l-95% CI u-95% CI eff.samp
units    0.4242 0.0002187     2.07     2400

 Location effects: Change ~ Order - 1
                    post.mean l-95% CI u-95% CI eff.samp  pMCMC
OrderCalanoida         6.920    4.910    8.671     5000 <2e-04 ***
OrderCyclopoida        9.308    3.748   14.940     5000 0.0020 **
OrderHarpacticoida     8.263    2.693   14.155     5000 0.0056 **  ---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1



### Effect of food availability on effect size estimates (order level);
### must re-run original code for matching tree to data file now
### including food
d<-read.table("Meta_Data_Food.txt",header=T)
attach(d)
```

```
### Set priors
prior <- list(R=list(V=1, nu=0.002),
G=list(G1=list(V=1, nu=1),
                    G2=list(V=1, nu=1),G3=list(V=1, nu=1)))

model.Food <- MCMCglmm(Change ~ Food,
random = ~ Order + Author + Species,
data = d, ginverse = list(Order = INtree$Ainv),
mev = d$Variance,
prior = prior,
nitt = 1000000,
thin = 100,
burnin = 500000)

summary(model.Food)

 Iterations = 500001:999901
 Thinning interval  = 100
 Sample size  = 5000

 DIC: -82.77589

 G-structure:  ~Order

      post.mean l-95% CI u-95% CI eff.samp Order
4.662  0.07475       17     5000

               ~Author

       post.mean l-95% CI u-95% CI eff.samp Author
7.329    1.537    15.51     4395

               ~Species

        post.mean l-95% CI u-95% CI eff.samp
Species     18.36     6.28    33.08     5000

 R-structure:  ~units
       post.mean  l-95% CI u-95% CI eff.samp
units    0.4901 0.0002083    2.526     2322

 Location effects: Change ~ Food
             post.mean l-95% CI u-95% CI eff.samp  pMCMC
(Intercept)     8.557    3.146   14.360     5000 0.0068 **
Foodstarved    -1.061   -6.791    4.116     5000 0.6960    ---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1



### Forestplot of copepod orders
rm(list=ls())
setwd("C:/Users/prsgu/Desktop/Meta/Meta-ana")
library(forestplot)
data<-read.table("order coef.txt",header=T)
attach(data)

row_names<-list(list("Harpacticoida","Cyclopoida","Calanoida"))
forestplot(row_names,mean=data$mean,lower=data$lower,upper=data$upper,boxs
ize=0.05,col=fpColors(all.elements="black"))
```

```
########## Phylogenetic meta-analysis of Calanoida families ##########

### Clean working environment
rm(list=ls())

### Load required packages
library(MCMCglmm)
library(ape)
library(phytools)

### Set working directory
setwd("C:/Users/Kyle/Desktop/Meta/Meta-ana")

### Read in and attach data
d<-read.table("Meta_Data_No_Food.txt",header=T)
attach(d)

### Create and attach Calanoida family tree
tree<-
'((Augaptilidae,(Heterorhabdidae,(Lucicutiidae,Metridinidae))),((((Temoridae
,(Acartiidae,Tortanidae)),Centropagidae),(Diaptomidae,Pseudodiaptomidae)),((
Paracalanidae,(Megacalanidae,Calanidae)),(Eucalanidae,Rhincalanidae),((Claus
ocalanidae,(Euchaetidae,Aetideidae)),Scolecitrichidae))));'

tree <- read.newick(text=tree)
attach(tree)

### Make tree ultrametric
tree <- compute.brlen(tree, method="Grafen")
is.ultrametric(tree)
plot(tree)

### Match tips to data
check.species<-function(x) {any(x==tree$tip.label)}
print(check.species)

### Apply above function and remove missing data; data file is a copy
### of the original data but without food to prevent unnecessary deletion of
### rows with NAs using the following.
d <- d[sapply(d[,"Family"],check.species),]

### Return complete columns
d  <-  d[complete.cases(d),]
print(head(d))

### Invert phylogenetic covariance matrix
INtree <- inverseA(tree, nodes="ALL")

### Set priors
prior <- list(R=list(V=1, nu=0.002),
G=list(G1=list(V=1, nu=1),
                     G2=list(V=1, nu=1),G3=list(V=1, nu=1)))

### Run model without moderators
Model.Family <- MCMCglmm(Change ~ 1,
random = ~ Family + Author + Species,
data = d, ginverse = list(Family = INtree$Ainv),
mev = d$Variance,
prior = prior,
```

```
nitt = 1000000,
thin = 100,
burnin = 500000)

summary(Model.Family)

 Iterations = 500001:999901
 Thinning interval  = 100
 Sample size  = 5000

 DIC: -84.80507

 G-structure:  ~Family

       post.mean l-95% CI u-95% CI eff.samp Family
2.161  0.07111    7.669     5000

               ~Author

       post.mean l-95% CI u-95% CI eff.samp Author
7.733    1.324    15.93     5279

               ~Species

        post.mean l-95% CI u-95% CI eff.samp Species
20.89    7.813    37.37     5000

 R-structure:  ~units
       post.mean  l-95% CI u-95% CI eff.samp
units    0.3882 0.0002443    1.898     2418
Location effects: Change ~ 1
            post.mean l-95% CI u-95% CI eff.samp  pMCMC
(Intercept)     6.671    3.819    9.378     5000 0.0012 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1



### Effect of dry weight on effect size estimates (family level)
model.DryWeight2 <- MCMCglmm(Change ~ DW,
random = ~ Family + Author + Species,
data = d, ginverse = list(Family = INtree$Ainv),
mev = d$Variance,
prior = prior,
nitt = 1000000,
thin = 100,
burnin = 500000)

summary(model.DryWeight2)

 Iterations = 500001:999901
 Thinning interval  = 100
 Sample size  = 5000

 DIC: -86.27415

 G-structure:  ~Family
        post.mean l-95% CI u-95% CI
eff.samp Family     2.289  0.06239      8.3
5000
```

```
               ~Author
        post.mean l-95% CI u-95% CI
eff.samp Author     7.951    1.401    16.34
5000

               ~Species
         post.mean l-95% CI u-95% CI
eff.samp Species      21.2    7.631    37.12
5000

 R-structure:  ~units
       post.mean  l-95% CI u-95% CI eff.samp
units    0.4137 0.0002301    2.158     2365

 Location effects: Change ~ DW
             post.mean l-95% CI u-95% CI eff.samp pMCMC
(Intercept)    6.9930   3.9696  10.1507     5239 0.002 **
DWyes         -0.4895  -2.9744   2.0941     5440 0.700    ---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1


### Calculate meta-analytical means of Calanoida families; saved as separate
### file
### Set priors
prior2 <- list(R=list(V=1, nu=0.002),
G=list(G1=list(V=1, nu=1),
                      G2=list(V=1, nu=1)))

model.Family.Fixed <- MCMCglmm(Change ~ Family - 1,
random= ~ Author + Species,
data=d, ginverse=list(Family = INtree$Ainv),
mev=d$Variance,
prior=prior2,
nitt=1000000,
thin=100,
burnin=500000)

summary(model.Family.Fixed)

 Iterations = 500001:999901
 Thinning interval  = 100
 Sample size  = 5000

 DIC: -88.05486

 G-structure:  ~Author
        post.mean l-95% CI u-95% CI
eff.samp Author     7.689    0.242    15.86
5000

               ~Species
         post.mean l-95% CI u-95% CI
eff.samp Species     25.76    8.117    49.02
4680

 R-structure:  ~units
       post.mean  l-95% CI u-95% CI eff.samp
units    0.4747 0.0001275    2.469     2169
```

```
 Location effects: Change ~ Family - 1

                        post.mean l-95% CI u-95% CI eff.samp  pMCMC
FamilyAugaptilidae         2.8975 -11.5871  16.7275     5000 0.6760
FamilyHeterorhabdidae    -13.2359 -29.4740   1.3728     5086 0.0956 .
FamilyLucicutiidae        10.5988  -2.5238  24.0999     5000 0.1180
FamilyMetridinidae         5.2315  -1.2217  11.6104     4757 0.1156
FamilyTemoridae            2.2549  -5.6422  10.0564     5000 0.5644
FamilyAcartiidae           7.2297  -0.1610  15.4353     4738 0.0668 .
FamilyTortanidae           3.0650 -11.0658  17.7045     5000 0.6724
FamilyCentropagidae        8.2648   3.1564  13.7041     5000 0.0044 **
FamilyDiaptomidae          7.9853  -3.7437  19.2448     5000 0.1660
FamilyPseudodiaptomidae    9.7213   2.0473  17.7061     5000 0.0236 *
FamilyParacalanidae       14.1040   0.3094  27.8249     5000 0.0448 *
FamilyMegacalanidae        2.3426  -6.6312  11.7383     4720 0.5996
FamilyCalanidae            6.1607   1.5442  10.4459     5000 0.0088 **
FamilyEucalanidae          3.0777  -3.1621  10.0271     5000 0.3628
FamilyRhincalanidae        9.4651   0.4080  19.2999     5000 0.0436 *
FamilyClausocalanidae      9.7440   3.7575  16.0750     5000 0.0032 **
FamilyEuchaetidae          1.7792  -7.4241  11.7061     5000 0.7024
FamilyAetideidae          10.4217  -2.5063  22.9102     5330 0.0960 .
FamilyScolecitrichidae    13.1919   2.6619  24.3506     5000 0.0240 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
### Effect of food availability on effect size estimates (family level);
### must re-run original code for matching tree to data file now
### including food
detach(d)
d<-read.table("Meta_Data_Food.txt",header=T)
attach(d)
prior <- list(R=list(V=1, nu=0.002),
G=list(G1=list(V=1, nu=1),
                     G2=list(V=1, nu=1),G3=list(V=1, nu=1)))

model.Food2 <- MCMCglmm(Change ~ Food,
random = ~ Family + Author + Species,
data = d, ginverse = list(Family = INtree$Ainv),
mev = d$Variance,
prior = prior,
nitt = 1000000,
thin = 100,
burnin = 500000)

summary(model.Food2)

 Iterations = 500001:999901
 Thinning interval  = 100
 Sample size  = 5000

 DIC: -74.24824

 G-structure:  ~Family

       post.mean l-95% CI u-95% CI eff.samp Family
2.298  0.08748     8.29     5000
```

```
               ~Author

       post.mean l-95% CI u-95% CI eff.samp Author
7.89    1.442    16.89     5000

               ~Species

        post.mean l-95% CI u-95% CI eff.samp Species
22.45    8.244    40.04     5000

 R-structure:  ~units
       post.mean  l-95% CI u-95% CI eff.samp
units    0.4284 0.0001658     2.25     2634
Location effects: Change ~ Food
             post.mean l-95% CI u-95% CI eff.samp  pMCMC
(Intercept)      8.829    1.454   16.406     4926 0.0236 *
Foodstarved     -2.061   -9.959    5.307     5186 0.5788   ---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1



### Forestplot of Calanoida families
rm(list=ls())
setwd("C:/Users/prsgu/Desktop/Meta/Meta-ana")
data<-read.table("family coef.txt",header=T)
attach(data)
library(forestplot)

row_names<-list(list("Scolecitrichidae","Aetideidae","Euchaetidae","Clausoca
lanidae","Rhincalanidae","Eucalanidea","Calanidae","Megacalanidae","Paracala
nidae","Pseudodiaptomidae","Diaptomidae","Centropagidae","Tortanidae","Acart
iidae","Temoridae","Metridinidae","Lucicutiidea","Heterorhabdidae","Augaptil
idae"))
forestplot(row_names,mean=data$mean,lower=data$lower,upper=data$upper,boxs
ize=0.25,col=fpColors(all.elements="black"))



########## Sensitivity analysis of positive effect sizes; negative effects
removed (family level) ##########

d<-read.table("Meta_Data_Positive.txt",header=T)

prior <- list(R=list(V=1, nu=0.002),
G=list(G1=list(V=1, nu=1),
                     G2=list(V=1, nu=1),G3=list(V=1, nu=1)))

model.positive <- MCMCglmm(Change ~ 1,
random = ~ Family + Author + Species,
data = d, ginverse = list(Family = INtree$Ainv),
mev = d$Variance,
prior = prior,
nitt = 1000000,
thin = 100,
burnin = 500000)

summary(model.positive)

 Iterations = 500001:999901
 Thinning interval  = 100
```

```
 Sample size  = 5000

 DIC: 114.405

 G-structure:  ~Family
       post.mean l-95% CI u-95% CI
eff.samp Family     1.891  0.06417    6.607
4750                ~Author
       post.mean l-95% CI u-95% CI
eff.samp Author     3.655  0.08374       10
2021

               ~Species
         post.mean l-95% CI u-95% CI
eff.samp Species     1.598   0.1051    4.529
3525

 R-structure:  ~units
       post.mean  l-95% CI u-95% CI eff.samp
units     2.552 0.0001689    6.936     1701

 Location effects: Change ~ 1
             post.mean l-95% CI u-95% CI eff.samp  pMCMC
(Intercept)     7.975    6.010    9.960     5000 <2e-04 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

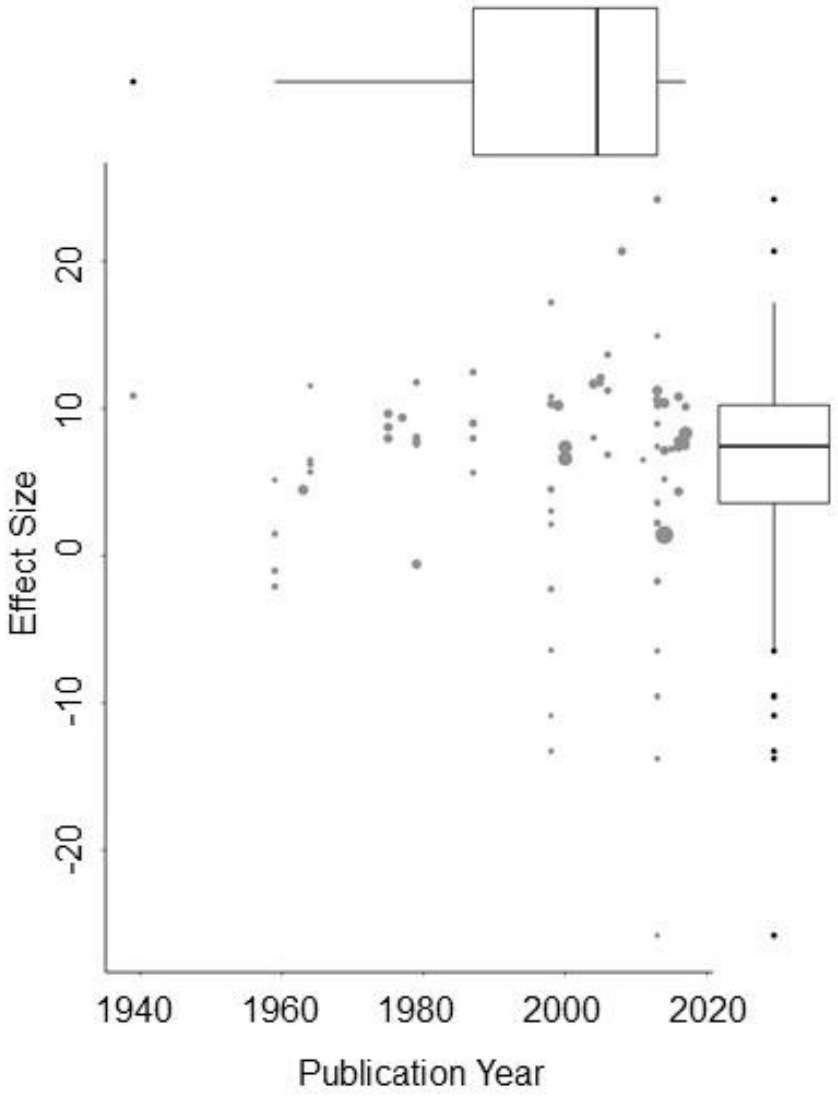
```
### Bubble plot of effect sizes and publication year to assess outliers
### and possible publication bias
library(ggplot2)
library(ggExtra)
p=ggplot(data, aes(x=Year, y=Change, color="black",
size=n))+geom_point()+theme(legend.position="none")+labs(x="Publication
Year", y="Effect Size")+
theme(panel.grid.major=element_blank(),panel.grid.minor=element_blank(),
panel.background=element_blank(),axis.line=element_line(colour="black"))
ggMarginal(p,type="boxplot")
```

```
### Funnel plot of effect sizes and standard error to assess asymmetry
### and possible publication bias
fun.plot<-rma(yi=Change,vi=Variance,data=d,method="REML")
fun.plot

Random-Effects Model (k = 78; tau^2 estimator: REML)

tau^2 (estimated amount of total heterogeneity): 18.3782 (SE = 3.9666)
tau (square root of estimated tau^2 value):      4.2870
I^2 (total heterogeneity / total variability):   96.90%
H^2 (total variability / sampling variability):  32.30

Test for Heterogeneity:
Q(df = 77) = 658.0071, p-val < .0001

Model Results:

estimate      se     zval    pval   ci.lb   ci.ub
```

```
  6.7120  0.5835  11.5033  <.0001  5.5684  7.8556  ***

---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

funnel(fun.plot, xlab="Percent Change", ylab="Standard Error",
yaxis="sei",level=c(90,95,99),back="white",shade=c("white","lightgray","dark
gray"), hlines="black")



### Overall test of heterogeneity of effect sizes between studies
library(metafor)

REM.auth.yr<-rma(Change, Variance, mods=~Author+Year, method="REML")
REM.auth.yr

Mixed-Effects Model (k = 78; tau^2 estimator: REML)

tau^2 (estimated amount of residual heterogeneity):     21.0636 (SE = 6.4911
)
tau (square root of estimated tau^2 value):             4.5895
I^2 (residual heterogeneity / unaccounted variability): 96.93%
H^2 (unaccounted variability / sampling variability):   32.57
R^2 (amount of heterogeneity accounted for):            0.00%

Test for Residual Heterogeneity:
QE(df = 46) = 227.2045, p-val < .0001

Test of Moderators (coefficient(s) 2:32):
QM(df = 31) = 35.8075, p-val = 0.2529

Model Results:

                             estimate         se     zval    pval       ci.lb
intrcpt                      146.1575  1238.1558   0.1180  0.9060  -2280.5834
AuthorAnraku                  -2.2064    29.4197  -0.0750  0.9402    -59.8681
AuthorAuel_et_al.              4.7807     8.5930   0.5564  0.5780    -12.0612
AuthorCass_and_Daly            1.3726     5.6796   0.2417  0.8090     -9.7592
AuthorCastellani_and_Altunbas -4.8874     6.7958  -0.7192  0.4720    -18.2069
AuthorCastellani_et_al.        5.1558     7.5470   0.6832  0.4945     -9.6360
AuthorClarke_and_Bonnet       -0.6428    44.8373  -0.0143  0.9886    -88.5222
AuthorCruz_et_al.              4.2062     6.6838   0.6293  0.5291     -8.8939
AuthorEpp_et_al.              -0.0367    20.8941  -0.0018  0.9986    -40.9884
AuthorGaudy_et_al.            -0.2799     8.8344  -0.0317  0.9747    -17.5949
AuthorGreen                   -0.2265    22.7972  -0.0099  0.9921    -44.9082
AuthorGreen_and_Chapman        0.5072    21.9570   0.0231  0.9816    -42.5277
AuthorHalcrow                 -5.3674    30.2698  -0.1773  0.8593    -64.6951
AuthorHirche                   0.6027    15.6243   0.0386  0.9692    -30.0205
AuthorIkeda                   -9.3038    21.0323  -0.4424  0.6582    -50.5264
AuthorIsla_and_Perissinotto    4.6734     7.8364   0.5964  0.5509    -10.6857
AuthorIsla_et_al.             13.9690     7.6373   1.8291  0.0674     -0.9998
AuthorKiko_et_al.              1.4297     6.4638   0.2212  0.8250    -11.2391
AuthorLehette                  4.0306     7.6443   0.5273  0.5980    -10.9521
AuthorLehette_et_al.           4.6382     7.2988   0.6355  0.5251     -9.6671
AuthorLi_et_al.                1.0180     5.8142   0.1751  0.8610    -10.3777
AuthorLiu_and_Ban              1.7887     6.7618   0.2645  0.7914    -11.4641
AuthorMcAllen                  2.8687     9.8599   0.2909  0.7711    -16.4564
                                ci.ub
intrcpt                     2572.8984
AuthorAnraku                  55.4552
AuthorAuel_et_al.             21.6227
AuthorCass_and_Daly           12.5044
AuthorCastellani_and_Altunbas  8.4322
AuthorCastellani_et_al.       19.9477
AuthorClarke_and_Bonnet       87.2367
AuthorCruz_et_al.             17.3063
AuthorEpp_et_al.              40.9151
AuthorGaudy_et_al.            17.0352
AuthorGreen                   44.4553
AuthorGreen_and_Chapman       43.5420
AuthorHalcrow                 53.9604
AuthorHirche                  31.2258
AuthorIkeda                   31.9189
AuthorIsla_and_Perissinotto   20.0325
AuthorIsla_et_al.             28.9378  .
AuthorKiko_et_al.             14.0984
AuthorLehette                 19.0132
AuthorLehette_et_al.          18.9436
AuthorLi_et_al.               12.4136
AuthorLiu_and_Ban             15.0415
AuthorMcAllen                 22.1937
```

```
AuthorPaffenhofer               3.7688     6.6851   0.5638  0.5729     -9.3337    16.8713
AuthorPascal_and_Chong         -1.8019     7.2325  -0.2491  0.8033    -15.9773    12.3736
AuthorRaymont                  -9.1360    32.5089  -0.2810  0.7787    -72.8523    54.5803
AuthorSvetlichny                1.5947     7.5139   0.2122  0.8319    -13.1324    16.3217
AuthorTeare_and_Price          -1.0443    20.7912  -0.0502  0.9599    -41.7942    39.7057
AuthorTeuber_et_al.            -4.5842     5.0350  -0.9105  0.3626    -14.4527     5.2843
AuthorThuesen_et_al.           -4.0324     9.4720  -0.4257  0.6703    -22.5971    14.5323
AuthorZervoidaki_et_al.         4.8422     7.1362   0.6785  0.4974     -9.1445    18.8289
Year                           -0.0694     0.6157  -0.1128  0.9102     -1.2762     1.1373

---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

S5 Bubble plot of publication year plotted against effect size to assess outliers and possible publication bias. Point size corresponds to the number of replicates per effect size.



S6 Citations of studies used in the meta-analysis.

Almeda R, Alcaraz M, Calbet A, Saiz E (2011) Metabolic rates and carbon budget of early developmental stages of the marine cyclopoid copepod *Oithona davisae*. Limnol Oceanogr 1:403-14

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

Auel H, Hagen W, Ekau W, Verheye HM (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 3:653-7

Cass CJ, Daly KL (2014) Eucalanoid copepod metabolic rates in the oxygen minimum zone of the eastern tropical north Pacific: Effects of oxygen and temperature. Deep Sea Res I 94:137-49

Castellani C, Altunbaş Y (2014) Seasonal change in acclimatised respiration rate of *Temora longicornis*. Mar Ecol Prog Ser 500:83-101

Castellani C, Robinson C, Smith T, Lampitt RS (2005) Temperature affects respiration rate of *Oithona similis*. Mar Ecol Prog Ser 285:129-35

Clarke GL, Bonnet DD (1939) The influence of temperature on the survival, growth and respiration of *Calanus finmarchicus*. Biol Bull 763:371-83

Cruz J, Garrido S, Pimentel MS, Rosa R, Santos AM, Ré P (2013) Reproduction and respiration of a climate change indicator species: effect of temperature and variable food in the copepod *Centropages chierchiae*. J Plankton Res 5:1046-58

Epp RW, Lewis WM (1979) Metabolic responses to temperature change in a tropical freshwater copepod (*Mesocyclops brasilianus*) and their adaptive significance. Oecologia 2:123-38

Gaudy R, Cervetto G, Pagano M (2000) Comparison of the metabolism of *Acartia clausi* and *A. tonsa*: influence of temperature and salinity. J Exp Mar Biol Ecol 1:5165

Green JD (1975) Feeding and respiration in the New Zealand copepod *Calamoecia lucasi* Brady. Oecologia 4:345-58

Green JD, Chapman MA (1977) Temperature effects on oxygen consumption by the copepod *Boeckella dilatata*. N Z J Mar Freshw Res 2:375-82

Halcrow K (1963) Acclimation to temperature in the marine copepod, *Calanus finmarchicus* (Gunner). Limnol Oceanogr 1:1-8

Hirche HJ (1987) Temperature and plankton. Mar Biol 3:347-56

Ikeda T (1979) Respiration rates of copepod larvae and a ciliate from a tropical sea. J Oceanogr Soc Jpn 1:1-8

Isla JA, Perissinotto R (2004) Effects of temperature, salinity and sex on the basal metabolic rate of the estuarine copepod *Pseudodiaptomus hessei*. J Plankton Res 5:57983

Isla JA, Lengfellner K, Sommer U (2008) Physiological response of the copepod *Pseudocalanus* sp. in the Baltic Sea at different thermal scenarios. Glob Change Biol 4:895-906

Kiko R, Hauss H, Buchholz F, Melzner F (2016) Ammonium excretion and oxygen respiration of tropical copepods and euphausiids exposed to oxygen minimum zone conditions. Biogeosciences 8:2241-55

Lehette P (2017) Respiration rates in tropical copepods: evidence of cold developmental acclimation? J Crustacean Biol 1:76-80

Lehette P, Ting SM, Chew LL, Chong VC (2016) Respiration rates of the copepod *Pseudodiaptomus annandalei* in tropical waters: beyond the thermal optimum. J Plankton Res 3:456-67

Li C, Sun S, Wang R, Wang X (2004) Feeding and respiration rates of a planktonic copepod (*Calanus sinicus*) oversummering in Yellow Sea Cold Bottom Waters. Mar Biol 1:149-57

Li W, Han G, Dong Y, Ishimatsu A, Russell BD, Gao K (2015) Combined effects of short-term ocean acidification and heat shock in a benthic copepod *Tigriopus japonicus* Mori. Mar Biol 9:1901-12

Liu X, Ban S (2017) Effects of acclimatization on metabolic plasticity of *Eodiaptomus japonicus* (Copepoda: Calanoida) determined using an optical oxygen meter. J Plankton Res 1:111-21

McAllen R, Taylor AC, Davenport J (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 A Mol Integr Physiol 2:195202

Paffenhöfer GA (2006) Oxygen consumption in relation to motion of marine planktonic copepods. Mar Ecol Prog Ser 317:187-92

Pascal L, Chong VC (2016) Does developmental temperature modulate copepods respiratory activity through adult life? J Plankton Res 5:1215-24

Raymont JE (1959) The respiration of some planktonic copepods. Limnol Oceanogr 4:479-91

Svetlichny L, Hubareva E, Isinibilir M (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 488:2431

Teare M, Price R (1979) Respiration of the meiobenthic harpacticoid copepod, *Tachidius discipes* Giesbrecht, from an estuarine mudflat. J Exp Mar Biol Ecol 1:1-8

Teuber L, Kiko R, Séguin F, Auel H (2013) Respiration rates of tropical Atlantic copepods in relation to the oxygen minimum zone. J Exp Mar Biol Ecol 448:28-36

Thuesen EV, Miller CB, Childress JJ (1998) Ecophysiological interpretation of oxygen consumption rates and enzymatic activities of deep-sea copepods. Mar Ecol Prog Ser 95-107

Zervoudaki S, Frangoulis C, Giannoudi L, Krasakopoulou E (2013) Effects of low pH and raised temperature on egg production, hatching and metabolic rates of a Mediterranean copepod species (*Acartia clausi*) under oligotrophic conditions. Mediterr Mar Sci 1:74-83