

Testing Bergmann's Rule in marine copepods

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Abstract

Macroecological relationships provide insights into rules that govern ecological systems. Bergmann's Rule posits that members of the same clade are larger at colder temperatures. Whether temperature drives this relationship is debated because several other potential drivers covary with temperature. We conducted a near-global comparative analysis on marine copepods (100,326 samples, 388 taxa) to test Bergmann's Rule, considering other potential drivers. Supporting Bergmann's Rule, we found temperature better predicted size than did latitude or oxygen, with body size decreasing by 44.7% across the temperature range (-1.7–30°C). Body size also decreased by 46.0% across the range in food availability and increased by 11.3% across high-predation to low-predation systems. Our results provide strong support for Bergman's Rule in copepods, but emphasises the

importance of other drivers in modifying this pattern. As the world warms, smaller copepod species are likely to emerge as “winners”, potentially reducing rates of fisheries production and carbon sequestration.

Introduction

Although much of ecology has focused on seemingly large differences among organisms and ecosystems, especially in terms of their spatial and temporal variation, the discipline has been criticised for lacking general unifying principles (McGill *et al.* 2006; Allen & Hoekstra 2015; O’Connor *et al.* 2019). Macroecology seeks to discover ecological principles by averaging over finer-scale variation to reveal large-scale statistical relationships (Brown & Maurer 1989; Lawton 1999; Gaston & Blackburn 2008). One such unifying principle is the importance of body size. Body size plays a central role in the physiology and ecology of organisms, governing processes such as respiration, metabolism, movement and trophic interactions (Peters 1986; Woodward *et al.* 2005; Yvon-Durocher *et al.* 2011). As a result, body size is increasingly used in ecosystem models to generalise traits across vast numbers of taxa, particularly in the marine environment (Blanchard *et al.* 2017). Better understanding global patterns of body size, and their drivers, will provide stronger unifying principles in ecology and help support development of ecosystem models.

One of the earliest relationships identified in ecology was formulated by Bergmann (1848) in German, although translation into English (Mayr 1956; James 1970) subsequently contributed to confusion surrounding its definition. Bergmann’s Rule has been tested and verified for many taxa, including mammals (Brown & Maurer 1989; Ashton *et al.* 2000), birds (James 1970; Ashton 2002), fish (Wilson 2009; Saunders & Tarling 2018), reptiles (Ashton & Feldman 2003; Angilletta *et al.* 2004), amphibians (Olalla-Tárraga & Rodríguez 2007), phytoplankton (Sommer *et al.* 2017), nematodes (Van Voorhies 1996), insects (Chown & Gaston 2010; Osorio-Canadas *et al.* 2016; Tseng & Soleimani Pari 2019), crustaceans (Manyak-Davis *et al.* 2013; Garzke *et al.* 2015; Leinaas *et al.* 2016) and planktonic ciliates (Wang *et al.* 2020). Yet the taxonomic level at which Bergmann’s Rule applies is commonly debated. Some theorists consider it to be intraspecific (Ashton *et al.* 2000; Olalla-Tárraga 2011), whilst others consider it interspecific (Blackburn *et al.* 1999; Hessen *et al.* 2013), leading to some confusion in the literature. Further, since the pattern was first described in endotherms, some question its applicability to ectotherms (Pincheira-Donoso *et al.* 2008; Watt *et al.* 2010). Here, we consider Bergmann’s Rule to be defined as (Bergmann 1848) himself defined it: species from the same taxonomic clade (here subclass) are generally smaller in warmer regions and larger in cooler regions. It is clear that regardless of the precise definition used, much can be gained by investigating Bergmann’s Rule (Olalla-Tárraga 2011) because spatial patterns in body size at all taxonomic levels strongly influence the ecology of a system (Peters 1986).

Commonly, temperature is considered the primary driver of Bergmann’s Rule, although some have argued that other drivers might modify the anticipated patterns across taxonomic groups (James 1970; Millien *et al.* 2006; Yom-Tov & Geffen 2011). This is because latitude (and therefore temperature) is confounded with light availability, oxygen concentration (in aquatic systems), predation rate and food availability (Ho *et al.* 2010). Of these, light is unlikely to be a direct driver of Bergmann’s Rule because many species that follow the pattern do not depend directly on light. However, primary productivity depends on light, which could in turn influence the food available for many groups. It is also likely that drivers of Bergmann’s Rule differ between endotherms and ectotherms. For endotherms, it is generally accepted that temperature is the selective mechanism driving Bergmann’s Rule, with species from cooler regions conserving heat by being larger and consequently having lower body surface-area-to-volume ratios (Mayr 1956; Hessen *et al.* 2013). But this is not true for ectotherms (Olalla-Tárraga *et al.* 2006; Watt *et al.* 2010). Ectotherms might benefit at cooler temperatures from increased cell sizes (Van Voorhies 1996; Hessen *et al.* 2013; Leinaas *et al.* 2016), selective protection from mortality, or increased fecundity, all of which scale with size (Yampolsky & Scheiner 1996; Vinarski 2014). Alternatively, the pattern might emerge as a result of a confounded driver such as oxygen concentration. For example, the ‘oxygen (limitation) hypothesis’ suggests that the size of marine ectotherms is limited by concentrations of dissolved O₂ (Chapelle & Peck 1999; Spicer & Morley 2019). Because gas solubility and water temperature are inversely correlated, this would predict larger sizes at cooler temperatures (Forster *et al.* 2012; Rollinson & Rowe 2018).

Food availability is another potential driver of Bergmann’s Rule, where more food can result in faster growth rates (Lin *et al.* 2013) and larger body sizes (Vidal 1980; Huston & Wolverton 2011; Andriuzzi & Wall 2018). Conversely, larger body sizes might be favoured in areas where food is scarce, because animals must forage further to find food (Belovsky 1997; Brown *et al.* 2017). Additionally, latitudinal variation in diet quality could further influence size (Berrigan & Charnov 1994; Ho *et al.* 2010).

Latitudinal variation in predation rate is also a plausible driver of Bergmann’s Rule within a taxonomic group (Wallerstein & Brusca 1982; Angilletta *et al.* 2004; Manyak-Davis *et al.* 2013) because predation rate tends to decline from the equator to the poles (Freestone *et al.* 2011). Predation rate could affect the size and growth of communities in several ways: through evolution towards species that mature at varied sizes (Kiorboe 2011; Manyak-Davis *et al.* 2013); through selective predator behaviour (Kiorboe 2011); through predation-related mortality prior to maximum size (Angilletta *et al.* 2004); and through selective advantages of allocating energy to predator defences (Kiorboe 2011).

We focus on Bergmann’s Rule in marine pelagic copepods, arguably the most abundant multicellular organism on Earth (Schminke 2007). Copepods are the primary link between phytoplankton and fish in aquatic systems, and they play a central role in fisheries production (Verity & Smetacek 1996). They are crustaceans that swim weakly and thus drift in currents. Marine copepods are an ideal group for testing Bergmann’s Rule in ectotherms because they are widespread over diverse environments, from the poles to the equator. There are a large number of copepod species, facilitating a more robust test of Bergmann’s Rule. Moreover, copepods are sensitive to many plausible drivers of Bergmann’s Rule, including temperature (Vidal 1980; Miller & Wheeler 2012), food availability (Rutherford *et al.* 1999; Miller & Wheeler 2012), predation (Kiorboe 2011; Miller & Wheeler 2012), oxygen concentration (Rollinson & Rowe 2018) and latitude (Tseng & Soleimani Pari 2019).

A search for Bergmann’s Rule in the literature on copepods returned no previous studies; however, Brun *et al.* (2016) investigated what has been called the Temperature-Size Rule (Atkinson 1994) in marine copepods. This rule describes the plastic phenotypic response to temperature within a species, with warmer temperatures leading to smaller individuals (Diamond & Kingsolver 2009; Ghosh *et al.* 2013). As the study actually compared the mean sizes of species and not individual sizes within a species, it effectively tested Bergmann’s Rule. Based on a varied dataset collected using many different nets, Brun *et al.* (2016) found that body size declined weakly at warmer temperatures, but there was little or no effect of temperature between 10–30degC. However, the temperature effect was dwarfed by the effect of food, which surprisingly led to a decline in body size with increasing food availability. This contrasts with many other studies that have shown increasing body size with food concentration in copepods (Vidal 1980) and other ectotherms (Pafilis *et al.* 2009; Huston & Wolverton 2011; Andriuzzi & Wall 2018). In a recent study, Evans *et al.* (2020) found marine copepods in the North Atlantic conform to Bergmann’s Rule. Although they found that temperature (2–27degC) had a more profound relationship with body size than described in Brun *et al.* (2016), they did not consider the effect of food availability. Other studies have found the intraspecific version of Bergmann’s rule (often called Temperature-Size Rule) holds true for several marine copepods species (Garzke *et al.* 2015; Leinaaset *et al.* 2016).

Here, we test whether food is a more important driver of body size than temperature in marine copepods, whilst considering other drivers of the potential relationships with body size, such as predation, and oxygen levels, which have not been investigated previously for copepods. We test these relationships simultaneously because they are likely partially confounded with one another, which could modify their perceived relationships with body size when tested independently. Further, we account for natural differences in size based on diet. These tests are facilitated at a near-global scale by virtue of the Continuous Plankton Recorder (CPR) survey dataset, the largest (>100,000 samples), most consistent (collected using the same device), global dataset on marine copepods (Richardson *et al.* 2006; Batten *et al.* 2019). We used a spatial comparative analysis to identify statistical relationships over environmental gradients across space (Brown 1995; Gaston & Blackburn 2008).

Material and methods

Sample collection

We chose the CPR dataset, assembled by the Global Alliance of CPR Surveys (Batten *et al.* 2019), because it provides the largest, consistent, most spatially-extensive, species-resolved plankton dataset (Richardson *et al.* 2006). Data were sourced from four surveys: the North Atlantic CPR Survey, the Scientific Committee on Antarctic Research (SCAR) Southern Ocean CPR Survey, the North Pacific CPR Survey, and the Australian CPR Survey (Fig. 1).

Although CPR surveys have better coverage in polar and temperate regions than in subtropical and tropical regions, samples have been collected in waters as warm as 30degC. All surveys use similar methods to collect and count copepods (see Reid *et al.* (2003), Richardson *et al.* (2006) for more details). Specifically, all CPRs use the same mesh size (270 μm), the same mesh material (silk), the same size mouth opening (1.61 cm^2), towed at the same depths (5-10 m), and have similar designs (Hosie *et al.* 2003; Reid *et al.* 2003). The CPR is mainly towed behind ships of opportunity on their normal trading routes, but also behind research vessels. Each CPR tow is usually up to 450 nautical miles. The internal silk roll that captures the plankton is cut up into samples representing either 5 or 10 nautical miles, and microscopic counts of copepods are converted to number per m^3 .

Copepod data

Copepods are identified to species whenever possible, and shared training and staff exchanges amongst surveys ensure comparable data. Names of all copepod taxa were updated using the World Register of Marine Species (WoRMS) (<http://www.marinespecies.org/>). Data were available for 388 taxa and from 100,326 samples.

To test Bergmann's Rule, we calculated the mean length of copepods in each sample and related this to environmental drivers. Maximum and minimum lengths of different copepod taxa were obtained from the Marine Planktonic Copepod Database from the Observatoire Océanologique de Banyuls-sur-Mer (<https://copepodes.obs-banyuls.fr/en/index.php>, Razouls *et al.* (2020)) and from Richardson *et al.* (2006). Because juveniles are more difficult to identify to species and reliably assign a size than adults, they were not included in the estimate of mean copepod size for each sample, although adults tend to be more common in CPR samples (Richardson *et al.* 2006). Each taxon was assigned a single size (the midpoint between their minimum and maximum lengths). We calculated the mean length of copepods in a CPR sample by multiplying abundance of adults of each taxon in the sample by their assigned length, and then dividing their sum by the total abundance of all adults within the sample.

Bergmann's Rule could also potentially be influenced by spatial differences in the trophic structure of communities because body size is linked to the ecological role of a species (Woodward *et al.* 2005; Yvon-Durocher *et al.* 2011). Because carnivorous copepods are generally larger than omnivorous ones (Mauchline 1998; Fig. S1 in Supporting information), which could affect observed relationships, we distinguished obvious differences in diets among taxa. We assigned a diet (carnivore or omnivore and herbivore combined, hereafter called omnivore) for each copepod taxon using a combination of dietary studies from the literature (see Richardson and Schoeman (2004)) and morphological differences in copepod mouthparts (Huys & Boxshall 1991). To calculate the proportion of omnivores we divided the summed abundance of omnivore within each sample by the total abundance of copepods within samples.

Environmental data

We used sea surface temperature (SST) as an estimate of ocean temperature for the near-surface CPR samples, and chlorophyll-*a* concentration (Chl-*a*) as a proxy for food availability to copepods. Chl-*a* is correlated with copepod growth and fecundity in herbivorous and omnivorous species (Richardson & Verheye 1998, 1999; Hirst & Bunker 2003; Bunker & Hirst 2004), and more Chl-*a* leads to more of these grazers and thus more carnivorous zooplankton (Richardson & Schoeman 2004). As *in situ* SST and Chl-*a* are not collected routinely on all CPR tows, we used remotely-sensed data. We matched the location and time of collection of CPR samples with estimates of SST and Chl-*a* averaged over eight days prior to sampling to

limit loss of data due to cloud cover and to represent feeding conditions over the recent past. For SST, we used daily Group for High Resolution SST data, a cloud-free global product based on satellite, buoy and ship data, and interpolated at 0.2degx0.2deg resolution (www.ghrsst.org). For surface Chl-*a* from September 1997 until the end of 2016, we used daily data from the European Space Agency Ocean Colour Climate Change Initiative data (esa-oceancolour-cci.org). Because this is a merged product from MERIS, Aqua-MODIS, SeaWiFS and VIIRS satellites, these data provide better coverage than products from a single satellite, and are more accurate globally (Melin *et al.* 2017). For 2017 and 2018, we combined data from Aqua-MODIS and VIIRS, the only available satellites. Chl-*a* data were retrieved at 4 km resolution and aggregated to 0.2degx0.2deg resolution to limit loss of data due to cloud cover and match the resolution of SST data. As there are no robust satellite Chl-*a* data before 1997, all analyses used CPR samples collected after this time.

We estimated predation rates on copepods by calculating the abundance of larger predatory invertebrates in CPR samples. We summed abundances of the primary invertebrate predators of copepods, including chaetognaths, amphipods, cnidarians, decapods, euphausiids and siphonophores. Although invertebrate predation is a crude indicator of total predation, it is collected concomitantly with the copepod data we used for the size analysis. We could not estimate potential fish predation because there is no global abundance dataset over time and space scales matching the CPR dataset.

To investigate whether oxygen is a driver of Bergmann's Rule (Forster *et al.* 2012; Rollinson & Rowe 2018), we used the World Ocean Atlas 2018 (WOA-18) (www.nodc.noaa.gov/OC5/woa18/). We had to use much coarser-resolution data (monthly climatology averaged at 1degx1deg resolution) because we could find no observed global oxygen product at a finer resolution.

Statistical analyses

To test Bergmann's Rule, we used a model-building approach. We fitted a weighted generalised linear mixed-effect model (GLMM, Bates *et al.* 2011), with fixed effects for all predictors (SST, Latitude, Oxygen, Chl-*a*, predator abundance, and the proportion of omnivores (Table S1). We included the proportion of omnivores in the model because omnivorous copepods are generally smaller than carnivorous ones (Fig. S1). Upon visual inspection of model residuals, their magnitude generally increased at higher fitted values. We thus used a gamma error structure with a log-link function (there were no zero values for size). Because estimates of mean length of copepods in a sample are more precise when there are more specimens, we weighted observations in the GLMM by the square-root of total copepod abundance within the sample.

To account for temporal and spatial correlation in the data, we used three random effects associated with the time and location of sampling. The first was a random intercept associated with differences amongst CPR surveys, which accounts for the use of different vessels, large-scale regional effects, and any minor methodological differences. The second was a random intercept of Tow within Survey, which adjusts for both temporal and spatial differences amongst tows. The last was a random slope for days elapsed on Tow within Survey, which accounts for spatiotemporal autocorrelation amongst samples on tows, which arises due to differing weather and collection conditions throughout the period of the tow. This helped remove any general linear trends over the period of the tow.

Due to the large number of samples (>100,000) and thus high statistical power, we did not assess the significance of predictors. Rather, we selected the best model using the Bayesian information criterion (BIC), which is based on the goodness of fit (log-likelihood ratio) relative to model complexity (number of parameters). BIC is suitable to fitting heuristic models with large numbers of observations; it more harshly penalising overfitting than commonly-used Akaike information criterion (Schwarz 1978; Aho *et al.* 2014).

From a preliminary analysis we found that SST, Latitude and Oxygen were strongly correlated (all $r > 0.59$, Fig. S2) and could not be included together in the model. We thus first assessed their relative importance in separate models with the other predictors (Chl-*a*, predator abundance, and proportion of omnivores), and then retained the most important variable amongst SST, Latitude and Oxygen for inclusion in subsequent analysis.

We used the pseudo R-squared described in Nakagawa & Schielzeth (2013) to estimate the proportion of variation explained by the gamma GLMMs (Nakagawa *et al.* 2017). To interpret the ecological relevance of the drivers, we evaluated effect sizes using expected relationships of the mean length with predictors (Nakagawa & Cuthill 2007; Sullivan & Feinn 2012). We also evaluated ecological relevance by converting copepod length estimates to body mass (using Wet-Weight (mg) = $0.03493 \times \text{Length (mm)}^{2.9878}$, Pearre Jr., 1980) because the food that is available to higher-level predators such as fish is related to body mass rather than size.

To assess the effect of influential points within the model, we performed sensitivity tests by iteratively identifying and removing groups of outliers and high-leverage observations; these procedures had no impact on overall results. Results presented thus include all available data. By mapping residuals globally both with and without random effects (Fig. S5), we confirmed that the use of random effects reduced spatial autocorrelation among samples; plotting residuals through time within Surveys and on Tows confirmed that our models reduced temporal autocorrelation. The code for the statistical analyses is publicly available on GitHub (www.github.com/maxcampb/Bergmann-Rule-Copepods).

Results

As judged by the BIC, and confirmed by the pseudo- R^2 , the mean length of copepods was more strongly related to SST than it was to Latitude or Oxygen concentration (Table 1). We found that in all cases, SST led to an improved fit (log-likelihood ratio, Table 1), so SST instead of Latitude or Oxygen concentration was used in all subsequent models.

The final model for mean copepod length included SST, Chl-*a*, Predation, and Proportion of Omnivores as predictors, and random effects for Survey, and Tow within. All predictors reduced BIC and increased the pseudo R-squared (Table 1). Together, fixed effects explained 64.2% of the variance in mean length of copepods (Table 1). Random effects explained a further 13.5%, where 1.8% was attributed to Survey (Fig. 2a), and 11.7% to the Tow within Survey effects (Fig. 2b).

The mean length of copepods declined with warmer SST (Fig. 2c), where the mean length of copepods decreased by a factor of 0.982 for each 1oC increase in SST, which is equivalent to a 0.83 mm decrease across the temperature range (-1.7–30oC) or a 44.7% decrease in mean length. This equates to an approximate linear decrease in copepod mass of ~2.6% per oC, equivalent to an 83.0% decrease in mass across the entire temperature range. Using a linear approximation, we found for each 1oC increase in temperature, the mean length of copepods was ~0.026 mm shorter.

The mean length of copepods also declined with increased Chl-*a* (Fig. 2d), where for each square increase in Chl-*a* (based on square-root transformation), the mean length of copepods decreases by a factor of 0.811. This is equivalent to a 0.78 mm decrease across the entire Chl-*a* range (0.02–9.51 mg.m⁻³) or a 46.0% decrease in mean length. This equates to an 84.1% decrease in copepod mass across the Chl-*a* range. Using a linear approximation, we estimate for each square increase in Chl-*a* that copepods are ~0.265 mm shorter.

Further, the mean length of copepods increased in samples with higher abundances of invertebrate predators (Fig. 2e), where for each e-fold increase in predator abundance (an increase by a factor of 2.718), the mean length increases by a factor of 1.011. This is equivalent to a 0.17 mm increase across the entire predation range, or an 11.3% increase in mean length. This equates to a 37.7% increase in copepod mass across the predation range. Using a linear approximation, we estimate for each e-fold increase in predator abundance, copepods were ~0.018 mm longer.

The mean length of copepods also decreased in samples that had a higher proportion of omnivorous copepods (Fig. 2f). The mean length was 2.34 mm or 61.6% smaller in samples comprising only omnivores when compared with samples comprising only carnivores. This equates to a 94.3% decrease in copepod mass.

Investigating the relative importance of fixed effects showed that both SST and Chl-*a* were of similar importance in determining the mean length of copepods, as indicated by their BIC and pseudo- R^2 . Removing

either of these substantially degraded BIC and pseudo- R^2 (Table 1). Removing Predation from the model resulted in a smaller decline in BIC and pseudo- R^2 (Table 1) and is thus less important in determining mean length than SST and Chl-*a*. Finally, removing the proportion of omnivores within samples degraded the BIC and pseudo- R^2 the most (Table 1).

Discussion

We believe that our study provides a robust test of Bergmann’s Rule because it is the largest study to date (based on 100,326 samples and 388 taxa within an order), is near-global in its distribution, and it applies a statistical approach that allows us to disentangle multiple correlated predictors. We show that marine copepods follow Bergmann’s Rule, with a strong decline in copepod body size with temperature, as reported by Evans *et al.* (2020). We also found that temperature was more important than latitude or concentration of dissolved oxygen, and that food availability was of similar importance to temperature, contrary to the findings by Brun *et al.* (2016), who found that body size was much more strongly related to food availability than to temperature. Nevertheless, our results corroborate findings by Brun *et al.* (2016) that copepod size decreases where more food is available. This contrasts with most previous work on copepods (Vidal 1980), nematodes (Andriuzzi & Wall 2018), lizards (Pafilis *et al.* 2009) and mammals (Huston & Wolverton 2011), which found that body size increases with food availability. We also found an increase in body size with increased abundance of predators, albeit that the effect size is small.

Explanations for Bergmann’s Rule

Although the mechanism underlying Bergmann’s Rule in copepods is unclear, it is apparent that the relationship with temperature is more than a spurious correlation driven by differences in food availability (McNab 1971; Belovsky 1997; Brown *et al.* 2017) or reduced predation rates in cooler environments (Wallerstein & Brusca 1982; Angilletta *et al.* 2004; Manyak-Davis *et al.* 2013). Even after these drivers are accounted for, a strong negative relationship between copepod size and temperature remains. We also found that dissolved oxygen concentration (which decreases with increasing temperature) does not adequately account for changes in size when compared with effects of temperature, suggesting that oxygen limitation is not responsible for Bergmann’s Rule. Instead, it is likely that copepod size is regulated directly by temperature. A potential mechanism is the negative correlation between growth efficiency and temperature, so that colder waters could produce larger copepods (Ikeda *et al.* 2001; Isla *et al.* 2008).

Our results suggest that when the negative relationship between taxon body size and temperature is adjusted for, the relationship between taxon body size and food availability is also negative. The direction of this relationship seems counterintuitive because typically more food leads to faster growth (Lin *et al.* 2013) and greater size (Vidal 1980; Berrigan & Charnov 1994). However, larger body sizes might allow copepods to undertake deeper vertical migrations in search of food or escape more visual predators in surface layers (Belovsky 1997; Brown *et al.* 2017). An alternative explanation is that copepods might grow larger in response to seasonality of their food supply (Brun *et al.* 2016). For example, copepods grow larger in systems with short seasonal pulses of food (e.g. Chl-*a*) by accumulating lipids for survival when food is limited (Kattner *et al.* 2007). Thus, being larger and having greater reserves could allow better survival during periods without food.

Increased abundance of invertebrate predators also translated to a modest increase in copepod size, a relationship not previously observed. This could be a selective advantage, where larger copepods might better resist invertebrate predators, and/or undertake deeper diel vertical migration to avoid predators (Ohman & Romagnan 2016). Because we estimated only relative abundance of invertebrate predators, predation by fish could also influence copepod size (Wallerstein & Brusca 1982).

Implications for climate change

The effect of temperature seems profound when considered across its range, with a 44.7% decrease in copepod length from -1.7 to 30°C. Bergmann’s Rule thus suggests that as oceans warm under climate change, the size

(and mass) of copepods is likely to decline (Walther *et al.* 2002). Under a high-emissions scenario (RCP8.5), SST is likely to warm by ~ 2.7 degC in 2090–2099 (compared to 1990–1999) based on the mean of the Coupled Model Intercomparison Project 5 (Bopp *et al.* 2013), or warm by ~ 0.6 degC under a low-emissions scenario (RCP2.6) (Bopp *et al.* 2013). Based on our statistical model, the effect of warming of ~ 2.7 degC under RCP8.5 could equate to a decrease in body mass of copepods globally of $\sim 7\%$. For RCP2.6, the ~ 0.6 degC warming could equate to a decrease in body mass of copepods globally of $\sim 1.5\%$. These estimates would translate to a similar decline in copepod biomass globally assuming abundance remains unchanged.

However, most Earth System models also project a decline in primary production and Chl-*a* (Bopp *et al.* 2013; Stock *et al.* 2014; Lefort *et al.* 2015; Galbraith *et al.* 2017; Woodworth-Jefcoats *et al.* 2017); decreases in primary production of between 2% and 16% by 2100 are predicted under RCP8.5 (Lefort *et al.* 2015). Using net primary production estimates from Bopp *et al.* (2013) and the conversion to Chl-*a* from Maranon *et al.* (2014), we find that under the RCP8.5 Chl-*a* is projected to decrease globally by ~ 0.086 mg m⁻³, and could lead to an increase in body mass of copepods globally by $\sim 2.5\%$. Under the RCP2.6, Chl-*a* is projected to decrease globally by ~ 0.020 mg m⁻³, and could lead to an increase in body mass of copepods globally by $\sim 0.6\%$. Thus, the combined effects of increased temperature and decreased Chl-*a* are likely to decrease global copepod biomass by $\sim 4.7\%$ under the RCP8.5, or decrease by $\sim 0.9\%$ under a RCP2.6. Current Earth System Models also project a future decline in zooplankton biomass (Woodworth-Jefcoats *et al.* 2017) – and copepods dominate zooplankton biomass (Verity & Smetacek 1996; Sommer *et al.* 2001) – by $\sim 7.9\%$ globally (Stock *et al.* 2014). This decline in copepod size and mass could negatively impact global fisheries (Sheridan & Bickford 2011). No Earth System Models consider the effect of Bergmann’s Rule on copepod size.

There could be several other important ecosystem consequences of copepod size following Bergmann’s Rule as the climate warms. Because swimming ability and thus the amplitude of their vertical migration is related to their size (Hays *et al.* 1994; Ohman & Romagnan 2016), a decline in body size with warming implies less extensive vertical migration. Thus, reductions in body size could potentially weaken the biological pump that transfers carbon from surface layers to the deep ocean (Cavan *et al.* 2019). Further, copepods significantly contribute to carbon exports via their sinking faeces and moults following ecdysis – at rates mostly determined by their body size (Stamieszkin *et al.* 2015). Therefore, reduction in copepod body size with warming could have significant ramifications for deep-ocean systems (Levin & Le Bris 2015; Sweetman *et al.* 2017) and for feedbacks to the climate system (Portner *et al.* 2019).

Final thoughts

There are now many studies that support Bergmann’s Rule – across marine (Saunders & Tarling 2018; Wang *et al.* 2020) and terrestrial systems (Arnett & Gotelli 2003; Ho *et al.* 2010) – and across ectothermic (Olalla-Tarraga & Rodriguez 2007; Wilson 2009) and endothermic taxa (Ashton *et al.* 2000; Brown *et al.* 2017). Despite this scientific support, there remains limited uptake of Bergmann’s Rule – and other macroecological ideas – in modelling studies. To project changes in biodiversity, ecosystems and fisheries under climate change, a host of modelling approaches are increasingly being coupled with Earth System Models (Everett *et al.* 2017), including nutrient-phytoplankton-zooplankton models (Stock *et al.* 2014), population models (Feng *et al.* 2018), size-spectrum models (Carozza *et al.* 2019), end-to-end ecosystem models (Griffith *et al.* 2011; Griffith *et al.* 2012) and statistical models (Grieve *et al.* 2017). There is considerable opportunity to include well-tested macroecological principles such as Bergmann’s Rule in future modelling efforts focused on climate change. Our analysis shows that these principles could substantially influence future projections.

This study also highlights the utility of using large global datasets for testing macroecological theory. Datasets such as the CPR that have been collected consistently for decades have predominantly been used to understand ecosystem dynamics or describe global change (Edward *et al.* 2010). There is great potential for comparative analyses with similar consistent, global datasets. Further, with the advent and increasing accessibility of powerful statistical techniques such as GLMMs – that make it possible to test multiple predictors whilst adjusting for spatial and temporal autocorrelation – there is increasing opportunity for providing robust and nuanced tests of macroecological relationships through spatial comparative analyses (Bolker *et al.* 2009). We recommend that future studies appropriately account for spatial and temporal

autocorrelation, and consider simultaneously testing as multiple potential predictors to avoid spurious and confounded relationships, as was common in the past.

There is still much to learn about Bergmann's Rule. Future research could be directed towards testing the rule across varied taxonomic levels, detailed investigations of regional differences, and testing nonlinear relationships between size and drivers of Bergmann's Rule. With directed research in this area, we could get closer to understanding and resolving the many complexities of Bergmann's Rule that have been debated for decades.

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Tables and Figures

Table 1. Step 1 compares three models with the WO18 data, to determine whether Latitude, Oxygen concentration or SST is the best predictor of size (n = 93,157). Step 2 compares five competing models to explain Bergmann’s Rule in marine copepods including only best temperature dependent predictor (SST, n=100,326). BIC was the basis for model selection, where lower values indicate a more parsimonious model. Additionally, log-likelihood represents the goodness of fit (lower is better), and degrees of freedom (df) used represents the complexity. All models have the same representation of random effects (Survey, and Tow within Survey intercept and slope).

Model	df	df	Log-likelihood	BIC	Pseudo-R ²	Pseudo-R ²
Step 1 models – WO18 data						

Model	df	df	Log-likelihood	BIC	Pseudo-R ²	Pseudo-R ²
Length ~ Latitude + Chl- <i>a</i> + Predation + Omnivore- proportion	10 10 10	10 10 10	-4349.9	8814.3	8814.3	0.52 0.58
Length ~ Oxygen + Chl- <i>a</i> + Predation + Omnivore- proportion			-4300.1	8714.5	8714.5	0.64
Length ~ SST(WO18 data) + Chl- <i>a</i> + Predation + Omnivore- proportion			-4232.4	8579.2*	8579.2*	
Step 2 models – Higher resolution data	Step 2 models – Higher resolution data					
Length ~ SST + Chl- <i>a</i> + Predation	9	9	-4908.4	9920.4	9920.4	0.52
Length ~ SST + Chl- <i>a</i> + Omnivore- proportion	9	9	-4519.8	9143.3	9143.3	0.63
Length ~ SST + Predation + Omnivore- proportion	9	9	-4658.9	9421.5	9421.5	0.53
Length ~ Chl- <i>a</i> + Predation + Omnivore- proportion	9	9	-4672.2	9448.1	9448.1	0.49
Length ~ SST + Chl- <i>a</i> + Predation + Omnivore- proportion	10	10	-4504.2	9123.7*	9123.7*	0.64

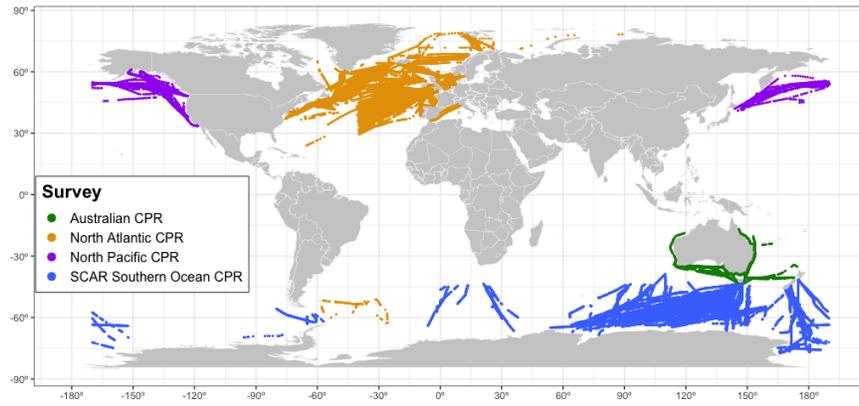


Figure 1. The Global Alliance of Continuous Plankton Recorder Surveys (GACS) sampling effort since September 1997. Different coloured lines represent sampling transects of individual surveys: the North Atlantic CPR Survey ($n = 54,176$), the SCAR Southern Ocean CPR Survey ($n = 36,501$), the North Pacific CPR Survey ($n = 4,674$), and the Australian CPR Survey ($n = 4,975$).

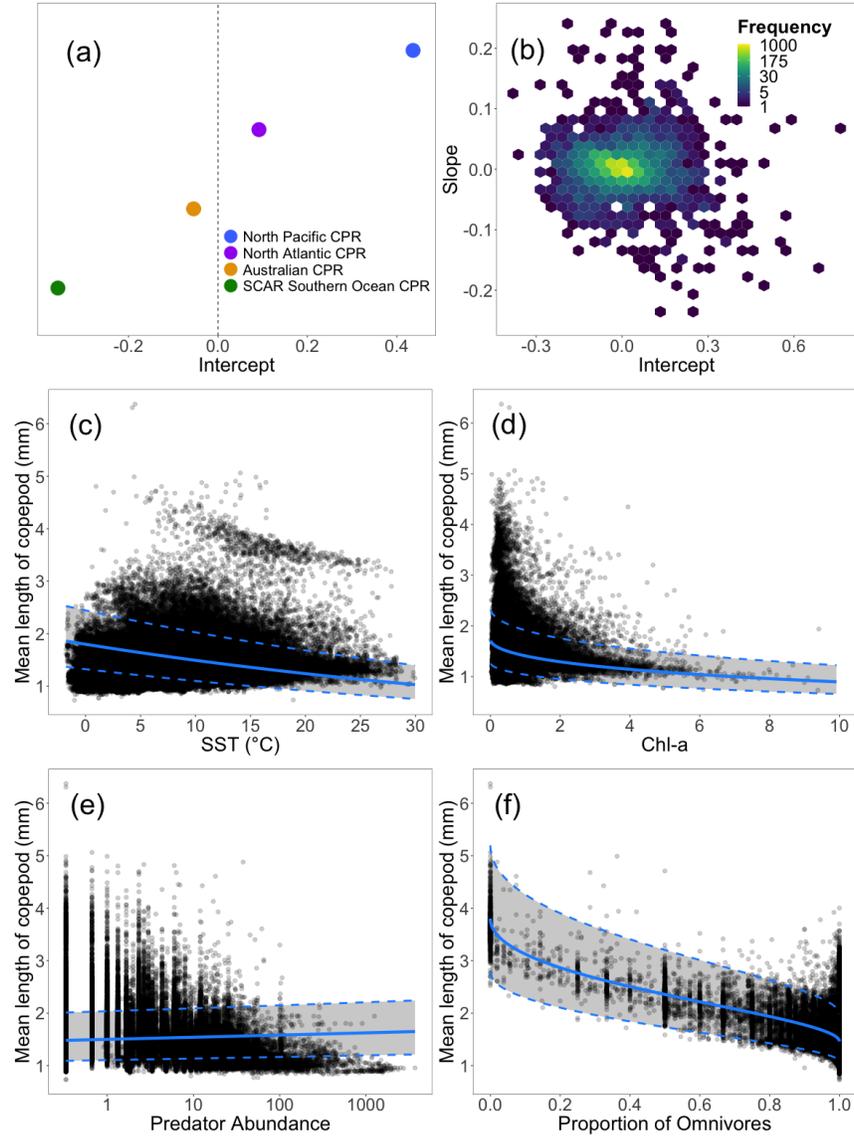


Figure 2. A visual summary of the GLMM for Bergmann's Rule showing relationships between mean length of copepods and (c) SST, (d) Chl-a, (e) abundance of invertebrate predators, and (f) proportion of omnivorous copepods. Blue solid lines represent expected values of mean length for each predictor, the grey band represents the 95% confidence interval for the expected values, and points are the observations. (a) The Survey random effect is shown with the intercepts and 95% confidence intervals (hidden by the mean estimate), and (b) the tow random effects, visualised with a hexplot of the random intercept and random slope for days elapsed ($n=100,326$).