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Lowri E Evans, Andrew G Hirst, Pavel Kratina, Grégory Beaugrand. Temperature-mediated changes in zooplankton body size: large scale temporal and spatial analysis. *Ecography*, 2020, 43 (4), pp.581 - 590. 10.1111/ecog.04631 . hal-04290544

HAL Id: hal-04290544

<https://hal.science/hal-04290544v1>

Submitted on 16 Nov 2023

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ECOGRAPHY

Research

Temperature-mediated changes in zooplankton body size: large scale temporal and spatial analysis

Lowri E. Evans, Andrew G. Hirst, Pavel Kratina and Grégory Beaugrand

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Ecography

43: 581–590, 2020

doi: 10.1111/ecog.04631

Subject Editor: Lisa Comte

Editor-in-Chief: Miguel Araújo

Accepted 12 November 2019



Climate warming has been linked with changes in the spatiotemporal distribution of species and the body size structure of ecological communities. Body size is a master trait underlying a host of physiological, ecological and evolutionary processes. However, the relative importance of environmental drivers and life history strategies on community body size structure across large spatial and temporal scales is poorly understood. We used detailed data of 83 copepod species, monitored over a 57-year period across the North Atlantic, to test how sea surface temperature, thermal and day length seasonality relate to observed latitudinal-size clines of the zooplankton community. The genus *Calanus* includes dominant taxa in the North Atlantic that overwinter at ocean depth. Thus we compared the copepod community size structure with and without *Calanus* species, to partition the influence of this life history strategy. The mean community body size of copepods was positively associated with latitude and negatively associated with temperature, suggesting that these communities follow Bergmann's rule. Including *Calanus* species strengthens these relationships due to their larger than average body sizes and high seasonal abundances, indicating that the latitudinal-size cline may be adaptive. We suggest that seasonal food availability prevents high abundance of smaller-sized copepods at higher latitudes, and that active vertical migration of dominant pelagic species can increase their survival rate over the resource-poor seasons. These findings improve our understanding of the impacts that climate warming has on ecological communities, with potential consequences for trophic interactions and biogeochemical processes that are well known to be size dependent.

Keywords: biogeography, body size, climate warming, continuous plankton recorder, seasonality, species distribution, temperature, traits, zooplankton

Introduction

Body size relates to the fitness, ecology and physiology of organisms, and is considered a master trait (Brown et al. 2004, Barton et al. 2013). Ectotherm body sizes change across time and space following changes in environmental conditions (Angilletta et al.



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2004, Kingsolver and Huey 2008). Laboratory experiments and meta-analyses have revealed that within ectothermic species body size co-varies strongly with temperature (Atkinson 1994, Horne et al. 2015) and can be influenced by seasonality in species with multiple generations per year (Horne et al. 2015). However, the influence of temperature and seasonality on ectotherm community size structure across large spatial and temporal scale is still understudied. Studies over large spatiotemporal scales accounting for species redistributions and local extinction may provide important insights into how community structure responds to ongoing climate warming (Stocker et al. 2014).

Interspecific patterns in body size distribution were first characterised by Bergmann (1847), who proposed that larger organisms of related species tend to be found at higher, and colder latitudes. Various taxonomic groups, such as marine mammals (Torres-Romero et al. 2016), follow such latitudinal–size clines. However, some taxa, such as bivalves, can exhibit the converse pattern to Bergmann’s rule, whereas no relationship is found in seabirds (Berke et al. 2013, Nunes et al. 2017). The mechanisms governing Bergmann’s rule are poorly understood, but multiple latitudinal drivers, including temperature, season length and food availability, are among the likely explanations (Blackburn et al. 1999, Watt et al. 2010). Seasonal variation in food availability and temperature is also associated with other environmental factors, such as variation in day length. All these seasonality components are known to influence body size distributions (Speirs et al. 2006).

Long-term monitoring programmes provide useful accounts of past and current distributions of organisms (Morán-Ordóñez et al. 2017). However, it is often challenging to predict the degree to which species will shift their distributions under a future warmer climate, as little is known about the drivers of their spatiotemporal rearrangement (Violle et al. 2014, Brun et al. 2016a). Shifting our focus from taxonomic composition to functional traits (such as body size), may determine more general patterns and mechanistically improve species distribution models (Purves et al. 2013). In particular, planktonic communities are ideally suited for examining the distribution of body size due to the availability of extensive spatiotemporal datasets. Zooplankton have been used to explore impacts of environmental change, as these animals have short lifespans, multiple generations a year and respond quickly to biotic and abiotic perturbations (Edwards and Richardson 2004, Kratina et al. 2014, Brun et al. 2016a). Plankton communities are critically important in marine ecosystems as the mediators of biogeochemical cycles and the flow of energy through marine food webs (Falkowski 1994, Roemmich and McGowan 1995, Turner 2004). Recent work has indicated that the distribution of plankton taxa has shifted spatially and temporally with ongoing climate change (Beaugrand et al. 2002). Although we have gained substantial insights into the plankton community size structure from studies restricted to small spatial scales (covering $<15^\circ$ of latitude) or short

time periods (<10 years) (Beaugrand et al. 2010, Chiba et al. 2015, Brun et al. 2016b), valuable new insights can be gained from the application of a robust analysis to the new extensive spatiotemporal data sets.

Analyses of community composition often consider a species-specific size distribution or size spectra in aquatic environments (White et al. 2007). Even if a latitudinal-size cline is observed, studies rarely consider the changes in these communities over time. Information about the magnitude of community body size changes, based on relative species abundance, and coupled with their life history strategies, could reveal finer details about the influence of climate warming on structure and dynamics of ecological communities (Atkinson 2006). Changes in the size structure may depend on specific characteristics of the species included. For example, community size structure can fluctuate due to high seasonal abundances of *Calanus* species, which have large body sizes, overwinter at depth and are therefore only seasonal residents of surface waters (Heath et al. 2004). The life history strategy of a species underlies its fitness and ultimately its survival (Hildrew et al. 2007, Kiørboe and Hirst 2008). If life history responses are adaptive and shift with environmental change, then the mechanisms governing latitudinal body size clines may also relate to adaptive strategies (Partridge and Coyne 1997). Active migration of dominant pelagic species and their overwintering strategies may be adaptive and modify spatiotemporal responses of plankton to climate warming. However, the impacts of such phenological or vertical shifts of plankton through the water column remain largely unexplored with respect to body size patterns.

Difference in body size structure is apparent between different ecosystems, such as between marine and freshwater plankton communities where nutrient conditions are expected to constrain growth (Litchman et al. 2009). More pronounced differences in species body sizes are found between aquatic and terrestrial ecosystems, where environmental temperature is thought to play a critical role. The difference in the temperature–size relationship between aquatic and terrestrial organisms suggests that oxygen supply is a key driver of body size changes (Atkinson et al. 2006, Forster et al. 2012). Oxygen supply and demand can vary among species, depending on individual body size, respiration apparatus and metabolism (Killen et al. 2010). Metabolism is a host of reactions and is related to both temperature and body size (Brown et al. 2004). Metabolic rates increase with warming (Gillolly et al. 2001, Brown et al. 2004), allowing faster juvenile growth rate and earlier maturity (Brown et al. 2004). A shorter juvenile phase thus results in a smaller adult body size, which reduces risk of predation and competitive ability (Gliwicz 1990). At higher temperatures, a smaller body size may be adaptive, as the metabolic rate tends to increase faster than the availability of oxygen increases with warming (Forster et al. 2012). However, delayed maturation at lower temperatures reduces the probability of successful reproduction (Angilletta et al. 2004). Therefore, gradients in body size likely depend on complex life history tradeoffs (Angilletta et al. 2004). Temperature changes may

also indirectly affect body size through trophic interactions (Gilbert et al. 2014). Phytoplankton are the main resource for zooplankton, while phytoplankton phenology is known to shift with temperature and be associated to seasonality (Edwards and Richardson 2004). Strong predation pressure can also alter the tradeoffs of their prey species (DeLong et al. 2015). Thus, body size modifications from species to communities may occur indirectly or directly through changes in environmental conditions.

The influence of temperature and seasonality on the community size structure of marine ectotherms can be explained either by the ‘resource availability hypothesis’ or by the ‘oxygen limitation hypothesis’. The ‘resource availability hypothesis’ suggests that body size co-varies with the length of the season, thus smaller-sized species are found at lower and higher latitudes (Geist 1987). This hypothesis is based on the observations that smaller-sized species might be prevalent at lower latitudes due to resource competition, whilst smaller-sized species may be abundant at higher latitudes due to resource shortages (Geist 1987, Blackburn et al. 1999). On the other hand, the ‘oxygen limitation hypothesis’ is based on the observation that metabolism is higher at lower and warmer latitudes, increasing individual cost of growth to a large body size, and resulting in a positive latitudinal–size cline or Bergmann’s rule (Atkinson et al. 2006). Partitioning between these two hypotheses remains an important challenge if we are to fully understand the changes in community size structure under ongoing climate warming.

Here, we employ the detailed continuous plankton recorder (CPR) dataset to investigate the community size structure of zooplankton over large spatiotemporal scales, in the context of climate warming. Specifically, we aim to: 1) establish whether the copepod community in the North Atlantic follows Bergmann’s rule; 2) examine whether *Calanus* species promote the overall community latitudinal–size cline with their life history tradeoffs (i.e. overwintering at depth); 3) describe the seasonal changes in copepod community size; and 4) determine how sea surface temperature, thermal seasonality and day length seasonality influence the copepod latitudinal–size clines and propose mechanistic explanations governing these patterns and wider consequences.

Material and methods

Copepod data compilation

We analysed the distribution of 83 copepod species in the North Atlantic Ocean, spanning between 30°N and 79°N of latitude and 70°W and 15°E of longitude, and the time period of 1958–2014. These data, comprising densities of copepods species and associated geographic coordinates, were provided by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) from their long term continuous plankton recorder (CPR). The samples were collected from CPR tows by ‘ships of opportunity’ at a water depth

of approximately 10 m and speed below 10 knots (Reid et al. 2003). The spatial distribution of these data is available in Supplementary material Appendix 1 Fig. A1. Some smaller species were not quantitatively sampled in the mesh. The CPR mesh size is 270 µm and efficient at collecting large zooplankton species (Batten et al. 2003), while the retention efficiency of smaller zooplankton species is lower than for the larger taxa. However, this approach still offers an insight into community size changes across large spatial and temporal scales, and other studies suggest that larger species or species of the upper size limit, tend to be more sensitive to temperature changes (Peck 2002). Detailed information about the collection of the CPR data and subsequent sample analysis is given in Batten et al. (2003) and Richardson et al. (2006). Body sizes for each of the 83 copepod species were obtained from published measurements, as adult female prosome length in millimetres (Supplementary material Appendix 1 Table A1). The copepods in this study spanned a size range from 1.3 mm (*Oculosetella gracilis*) to 10 mm (*Paraeuchoeta glacialis*).

Environmental data compilation

Sea surface temperature (SST) was obtained from the Comprehensive ocean-atmosphere data set (COADS), as a 1-degree enhanced dataset provided by the National Oceanic and Atmospheric Administration, Cooperative Institute for Environmental Research in Environmental Sciences Climate Diagnostics Center Database, Boulder, Colorado (Woodruff et al. 1987). The SST data were gridded to a resolution of 1° longitude × 1° latitude to correspond to the spatial resolution of the copepod abundance data. The SST ranged between 2 and 27°C across the study area and the mean temperatures were typically lower at higher latitudes. Thermal seasonality was estimated from the SST dataset by taking the temperature range (mean maximum temperature minus the mean minimum temperature for each spatial sampling point) per month, to the same resolution as the copepod abundance data. The day length in hours was used to consider day-length seasonality and was determined from the date and latitude of each sample by using the day length function in MATLAB (Wiens 2015), at the same spatiotemporal resolution as the copepod abundance data. All datasets were compiled and prepared in the form of a matrix for analyses using MATLAB R2015a 9.0.

Statistical analyses

Mean body size of the copepod community

The copepod community body size (mm) or CCS, was estimated for each CPR sample, as an abundance weighted mean prosome length, considering all copepods in the sample. Previous studies have suggested that CCS is a good indicator of zooplankton functional diversity (Beaugrand 2005, Chiba et al. 2015). For each CPR sample (number of samples, $n = 223\ 006$), CCS was estimated by the prosome length L_j of adult females (mm) of each species j ($1 \leq j \leq s$), their

corresponding abundances (number of individuals per sample) n_j , and overall species abundance (s) in the community, as:

$$\text{CCS} = \frac{\sum_{j=1}^s (L_j n_j)}{\sum_{j=1}^s n_j} \quad (1)$$

Females were chosen to represent species body size as this sex numerically dominates populations for many copepods (Rombouts et al. 2009, Chiba et al. 2015). The range and abundances of copepod developmental stages were not known. Therefore, this measure does not give an indication of the actual full ontogenetic size structure of the community. However, this approach provides a reasonable proxy for the size composition and the relative dominance of large to small species in the community (Beaugrand 2009). Prior to all analyses CCS data were \log_{10} transformed to ensure that changes in relative sizes were comparable.

The CCS was then calculated for all species (number of species, $n=83$), for all species with *Calanus* species removed (number of species with *Calanus* removed, $n=79$), and also for all species with *Calanus hyperboreus* removed (number of species with *C. hyperboreus* removed, $n=82$). The comparison of data with and without *Calanus* species allowed us to partition the importance of life history strategy (specifically their ability to over-winter out of surface waters and at great depth). The comparison of data with and without *C. hyperboreus* allowed us to determine whether the community level results are influenced by this most abundant species.

The mean, maximum and minimum CCS were calculated across the 57-year period to evaluate the change in CCS over the seasons (based on the temperate Northern Hemisphere classifications of spring, summer, autumn and winter) within a year. Potential differences in CCS between the seasons were determined using an ANOVA. Levene's test for equality of variance was used to determine whether variation between months was significantly different for the mean, minimum and maximum CCS.

Relationship between CCS and key environmental variables

The degree of collinearity between the following pairs of variables was assessed using a third-order partial correlation analysis: 1) latitude, 2) longitude, 3) CCS, 4) SST, 5) thermal seasonality and 6) day-length seasonality, whilst controlling for all remaining pairs within a matrix. This was undertaken for CCS (all species), CCS with *Calanus* species removed and for CCS with *C. hyperboreus* alone removed, allowing us to determine which environmental variables were mainly associated with the temporal variability in CCS.

The strongest predictors of CCS distribution were determined by the coefficient of determination (R^2) from a single-term exponential model. The rates of CCS change (per year) were calculated and compared to environmental change over the same period. Within each grid cell (1° latitude \times 1°

longitude) the rate of change for CCS and SST per year was interpolated using the inverse squared distance technique (Beaugrand and Ibañez 2002) and calculated as the slope of the regression of average monthly CCS and SST values within each year over the 57-year time period. This was repeated for CCS data with and without *Calanus* species and with and without *C. hyperboreus*. A second-order polynomial was used to model the data, as the relationship between variables was curvilinear. The fit of the polynomial model provides an improved (higher) R^2 value over a linear model, whilst the residuals were patchy with grouped negative and positive sections confirming a non-linear relationship.

The comparison of partial correlation coefficients and the fit of standard linear regression were two different but complementary approaches to the analysis. Partial correlation analysis indicates how x- and y-variables are associated once other variables are controlled for (Beaugrand and Kirby 2010). On the other hand, linear regression determines how y (dependent variable) may be statistically predicted from x (independent variable). These analyses may highlight different outcomes, depending on the shape of the relationship. If there is a linear relationship between variables, then the outcome of both analyses should be similar. However, both analyses may highlight different associations in the case of a non-linear relationship between variables (Montgomery et al. 2010).

To determine the influence of climate warming on CCS, to separate the temporal patterns of variability in CCS from spatial variability, and to highlight any long-term trends in this metric, we used a standardised principal component analysis (PCA). This approach has been used previously to analyse changes in the CPR dataset and is well suited to non-uniform but large datasets (Beaugrand et al. 2001, Beaugrand and Reid 2003, Reid et al. 2016). PCA was used to summarise the large datasets and highlight the main patterns that emerged, by focusing on areas within the aforementioned $1 \times 1^\circ$ grid that contained at least five data points. PCA was performed on the CCS and SST values per $1 \times 1^\circ$ grid cell. A new set of characteristics were constructed based on the original data values which focused on the variance in the data, called the eigenvectors and the principal components. Eigenvectors were used to investigate the relationships between CCS and SST over spatial scales, as they provided a relative measure of the direction of the data, such as if an area is mainly cooling or warming in temperature. Individual principal components of these CCS and SST were used to examine the temporal associations in the data, as the slope of regression of mean monthly values within each year over a 57-year period. Temporal autocorrelation does not influence PCA (Reid et al. 2003, 2016) and the pre-analysis of residuals did not indicate spatial autocorrelation (Supplementary material Appendix 1 Fig. A3). Further information on the use of PCAs with CPR data can be found in Beaugrand et al. (2003).

Results

Copepod community body size (CCS) in the North Atlantic was strongly and positively correlated with latitude ($R^2 = 0.6$,

$p < 0.0001$, $n = 4300$). CCS increased by 0.1 mm per °latitude ($p < 0.0001$, Fig. 1a), whereas the mean SST decreased by 0.3°C per °latitude ($p < 0.0001$, Fig. 1b). These marine pelagic copepods therefore follow Bergmann's rule, with larger sized species being more abundant at higher latitudes in comparison to smaller sized species (Fig. 1a).

Monthly distribution of copepod community body size (CCS) across the North Atlantic differed among the seasons (ANOVA, $p < 0.05$, $F = 528.36$, $n = 684$, Fig. 2). This also highlights the influence of *Calanus* species that move out of the surface zooplankton community when they overwinter at depth. The maximum CCS for all species declines slightly in late summer (Fig. 2a), the mean CCS increases slightly in mid-summer compared to the rest of the year (Fig. 2b), whilst there is an increase in the minimum CCS during late summer and early autumn, with decreases in minimum CCS in mid-winter and spring (Fig. 2c). Indeed, CCS with *Calanus* removed remains fairly constant across mean, minimum and

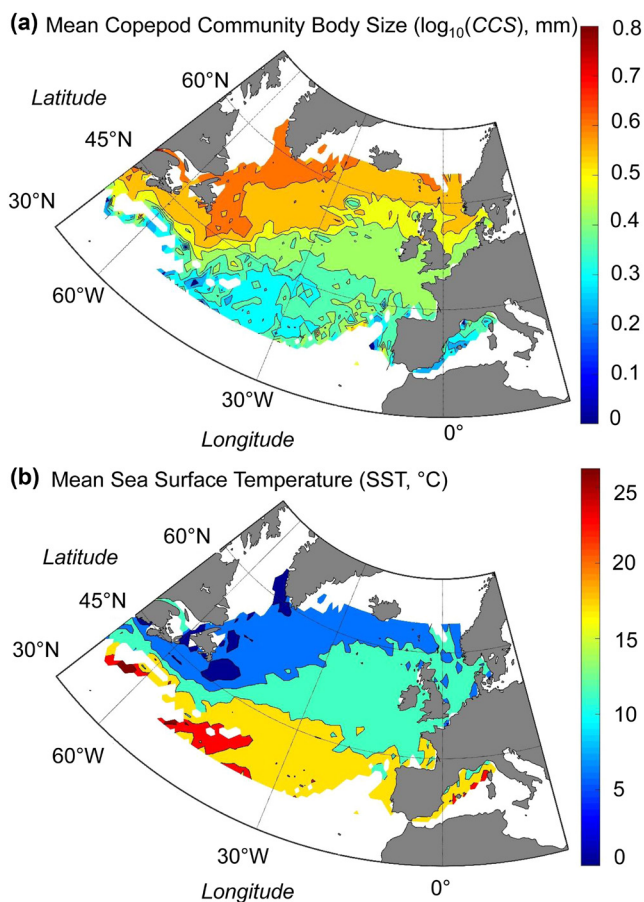


Figure 1. (a) The distribution of copepod community body size \log_{10} (CCS, mm) between 1958 and 2014 across the North Atlantic. A gradient in mean community body size is apparent, with smaller copepod species most common at lower latitudes. (b) Mean sea surface temperature (SST, °C) between 1958 and 2014, indicating a marked temperature gradient across latitude with warmer waters occurring to the south.

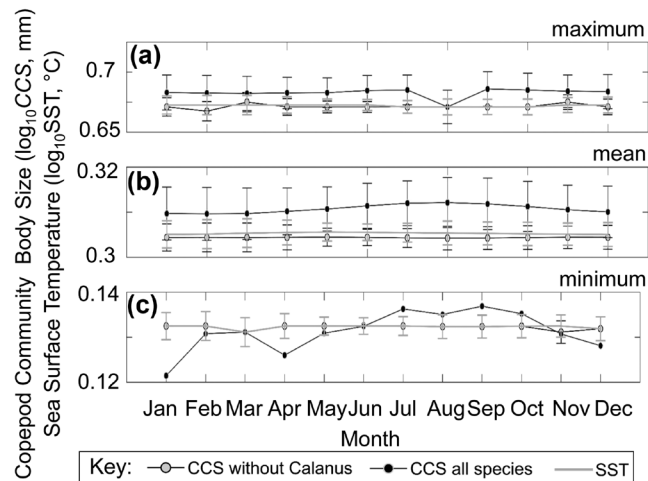


Figure 2. The monthly distribution of (a) maximum, (b) mean and (c) minimum copepod community body size (\log_{10} CCS, mm) and sea surface temperature (\log_{10} SST, °C). All species are illustrated as black data points, whereas data points with *Calanus* species removed are grey. The monthly CCS remain constant alongside monthly SST for the maximum, mean and minimum, whereas the CCS for all species fluctuates across months. The monthly variation in CCS is significant (ANOVA, $p < 0.05$, $F = 528.36$, $n = 684$).

maximum sizes throughout the year, which is very similar to the pattern in mean SST across seasons (Fig. 2a–c).

The third-order partial correlation analysis showed strong relationships between CCS, SST ($r_{34.1256} = 0.74$, $p < 0.0001$, $n = 4300$), day length seasonality ($r_{36.1245} = 0.96$, $p < 0.0001$, $n = 4300$) and thermal seasonality ($r_{35.12456} = 0.72$, $p < 0.0001$, $n = 4300$). The removal of *Calanus* species resulted in stronger associations between CCS, SST ($r_{34.1256} = 0.81$, $p < 0.0001$, $n = 4300$) and thermal seasonality ($r_{35.1246} = 0.74$, $p < 0.0001$, $n = 4300$), but weaker association between CCS and day length seasonality ($r_{36.1245} = 0.93$, $p < 0.0001$, $n = 4300$). Weak relationships were apparent between CCS and longitude when considering all species ($r_{23.1456} = 0.06$, $p < 0.0001$, $n = 4300$), all species but with *Calanus* removed ($r_{23.1456} = 0.01$, $p < 0.0001$, $n = 4300$) and all species but with *C. hyperboreus* removed ($r_{23.1456} = 0.05$, $p < 0.0001$, $n = 4300$). Overall relationships between CCS with *C. hyperboreus* removed were very similar to all species CCS (e.g. CCS with SST ($r_{34.1256} = 0.75$, $p < 0.0001$, $n = 4300$)).

Latitude was a strong predictor of CCS distribution (polynomial regression; $R^2 = 0.63$, $p < 0.0001$, $n = 4300$, Fig. 3a), but it was a weaker predictor of CCS when *Calanus* species were removed (polynomial regression; $R^2 = 0.4$, $p < 0.0001$, $n = 4300$, Fig. 3b). Although significant, longitude was a poor predictor of CCS distribution (linear regression; $R^2 = 0.0004$, $p < 0.0001$, $n = 4300$, Supplementary material Appendix 1 Fig. A2a–b). *Calanus* species appeared to strengthen the latitudinal-size cline at the upper limits of CCS at higher latitudes (>68°N) and at mid-latitudes (35–50°N) (Fig. 3a). The main predictor of CCS was SST, as it explained a higher proportion of the variance (polynomial regression; $R^2 = 0.8$, $p < 0.0001$, $n = 4300$, Fig. 3c), than latitude, day-length

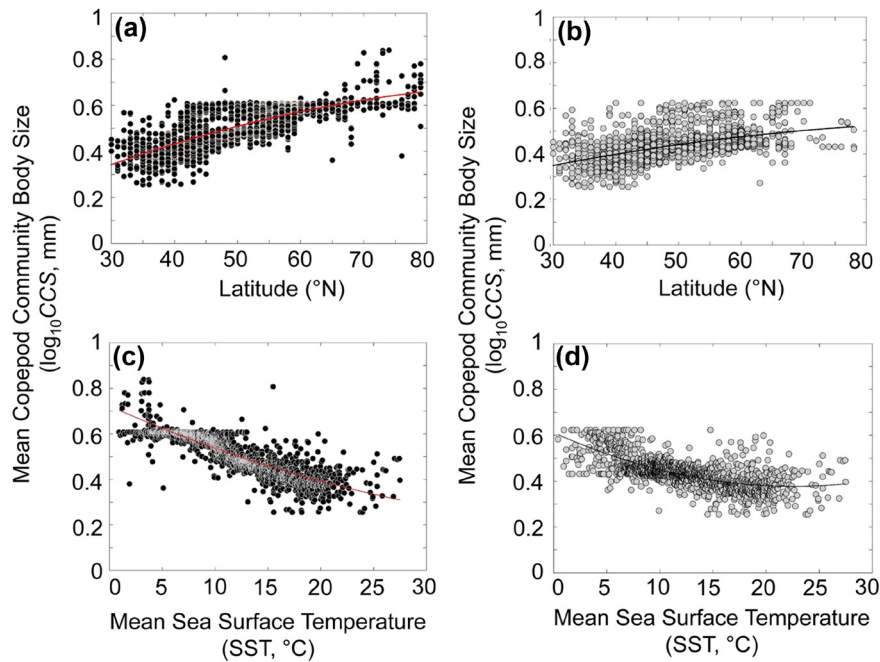


Figure 3. The relationship between copepod community body size and latitude ($^{\circ}\text{N}$) per $1 \times 1^{\circ}$ grid cell in the North Atlantic between 1958 and 2014 with (a) all species in black data points and (b) with *Calanus* species removed in grey data points. There is a significant correlation between body size (CCS, mm) and latitude (lat, $^{\circ}\text{N}$) for (a) all species ($R^2=0.65$, $p < 0.0001$, $n = 4300$, $\text{CCS} = -0.01\text{lat}^2 + 0.1\text{lat} + 0.5$) and (b) with *Calanus* species removed ($R^2=0.4$, $p < 0.0001$, $n = 4300$, $\text{CCS} = 0.002\text{lat}^2 + 0.04\text{lat} + 0.44$). A higher proportion of the variability in CCS is explained by a latitudinal driven variable when *Calanus* species are included. The relationship between mean sea surface temperature and copepod community size per $1 \times 1^{\circ}$ grid cell in the North Atlantic between 1958 and 2014 with (c) all species in black and (d) with *Calanus* species removed in grey. There is a significant negative correlation between community body size (CCS) and temperature (T) for (c) all species ($R^2=0.8$, $p < 0.0001$, $n = 4300$, $\text{CCS} = 0.01\text{T}^2 - 0.1\text{T} + 0.5$) and (d) with *Calanus* species removed ($R^2=0.6$, $p < 0.0001$, $n = 4300$, $\text{CCS} = 0.01\text{T}^2 - 0.1\text{T} + 0.4$). A higher proportion of the variability in CCS is explained by sea surface temperature when *Calanus* species are included.

seasonality ($R^2=0.3$, $p < 0.0001$, $n = 4300$) and thermal seasonality ($R^2=0.02$, $p < 0.0001$, $n = 4300$). Once *Calanus* species were removed SST remained the best predictor, as it explained a higher proportion of the variance in CCS (polynomial regression; $R^2=0.6$, $p < 0.0001$, $n = 4300$, Fig. 3d), compared to latitude alone or day-length seasonality ($R^2=0.01$, $p < 0.0001$, $n = 4300$) and thermal seasonality ($R^2=0.1$, $p < 0.0001$, $n = 4300$).

The mean changes in SST suggests that the eastern North Atlantic was primarily warming, but that the western part was primarily cooling, as highlighted by the positive and negative eigenvectors (Fig. 4a–b). This was also reflected in the CCS distribution, with larger body sizes being more common in the cold regions. Moreover, CCS and SST were correlated over the years 1958 to 2013 (PCA, $p < 0.0001$, $n = 56$). The first principal component of CCS (48% of the total variance) positively co-varied with the first principal component of SST (51% of the total variance) (Fig. 4c). First normalised eigenvector of CCS demonstrated a negative relationship between SST and CCS. When year-to-year variability was removed by using a first order moving average, sea surface temperature became an even stronger predictor of CCS ($R^2=0.83$, $p < 0.001$, $n = 56$, Fig. 4d). This suggests that a large proportion of the data correlate well regardless

of the strong correlation between mean values, as using PCA reduces the risk of overfitting when using linear models.

Discussion

We demonstrate that copepods in the North Atlantic follow Bergmann's rule, with larger species being more common at higher latitudes. The presence of *Calanus* species acts to strengthen this latitudinal-size cline, due to their large body sizes and the tendency of this genus to occupy higher latitudes. There was a seasonal shift in copepod community body size structure, while mean body size was relatively constant throughout the year, the minimum and maximum body sizes changed on a seasonal basis. Mean CCS was negatively related to sea surface temperature, and the thermal seasonality and day-length seasonality had weaker influence. Previous work that only considers mean annual values thus overlooks these important seasonal changes in community size structure (Boersma et al. 2016).

Many ectotherms, including fish, turtles, lizards, insects and phytoplankton, are known to follow Bergmann's rule (Belk and Houston 2002, Angilletta et al. 2004, Sommer et al. 2016). However, quantitative test of latitudinal size clines

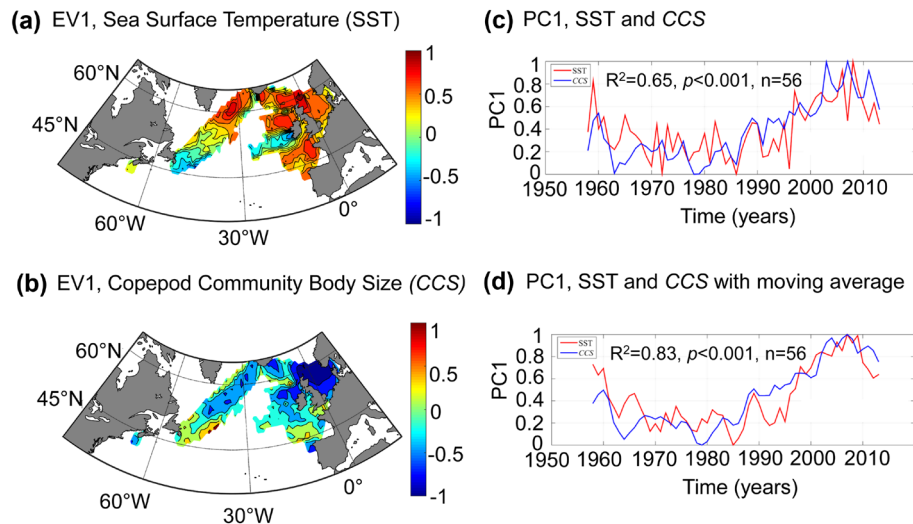


Figure 4. Outputs from principal component analysis on copepod community size (CCS) and sea surface temperature (SST). (a) First normalised eigenvector (EV1) for SST (51% of the variability). (b) First normalised eigenvector (EV1) for CCS (48% of the variability). (c) Correlation between principal component 1 (PC1) of SST (red) and principal component 1 (PC1) of CCS (blue) with Pearson correlation coefficient indicated without a moving average. (d) Correlation between smoothed (moving average of 10 months) principal component 1 (PC1) of SST (red) and (moving average of 10 months) principal component 1 (PC1) of CCS (blue) with Pearson correlation coefficient indicated. In (d), a moving average of 10 months, which allows for the inclusion of a large proportion of the dataset but reduces the influence of any strong outliers, was performed to account for the seasonality in the data.

of marine ectotherms has never been undertaken over such large spatiotemporal scales as in our study (a 57 year time period over a continuous 40° of latitude). We showed that smaller pelagic copepods are favoured in the warmer areas, in agreement with studies focused on other taxa (Blanckenhorn 2000, Daufresne et al. 2009, Morán et al. 2010). Latitudinal body size patterns were strengthened (higher R^2 value and a steeper slope) when *Calanus* species were included in the analysis. This provides a unique insight into the influence of their seasonal strategies of overwintering at depth when food is scarce (Marshall and Orr 1955, Hind et al. 2000). This indicates that Bergmann's rule may be governed by adaptive mechanisms, as the seasonal changes in CCS are associated with the presence of species with certain life history traits and thermal tolerances. Although the abundance of small species of *Calanus*, namely *C. helgolandicus*, has been increasing over time (Fromentin and Planque 1996), a larger species, *C. finmarchicus*, has been declining (Fromentin and Planque 1996), and these changes seem to be linked to their thermal niches (Helaouët and Beaugrand 2007). Body sizes of taxa used in this analysis were not directly measured in-situ and therefore we could not explore intraspecific body size changes across temporal and latitudinal gradients. The temperature–size rule describes the intraspecific response of ectotherms, which mature at smaller body sizes when developing in a warmer environment (Atkinson 1994). These intraspecific responses can also reduce mean community body size at higher temperatures and remain a promising avenue for future research.

Seasonality is another important factor that can potentially influence the geographical distribution of ectotherm body size (Atkinson 1994, Valenzuela-Sánchez et al. 2015).

For instance, seasonal variation in average copepod body size between 1 and 5 mm was recorded by Brun et al. (2016b). Day-length and thermal seasonality were closely related to the copepod body size clines in the North Atlantic. Greater temperature range over the season is associated with a larger range of copepod body sizes in temperate waters. There was also higher variation in CCS in highly seasonal day-length areas. However, when *Calanus* species were removed, the relationships between body size and day-length seasonality weakened. The smaller species were uncommon at higher latitudes, likely due to lower survival during winter periods with low food availability. An increase in maximum CCS during winter months (Fig. 2) is contrary to what is expected, in particular if this was driven by *Calanus* species as they commonly overwinter at depth. However, this increase in CCS was driven by another large Arctic species, *Paraeuchaeta glacialis*, which remains in shallow water during the winter and has the highest feeding activity during the night (Matsuno et al. 2015). Populations of *P. glacialis* may therefore be lingering in surface waters, during long winter nights (Planque and Batten 2000). The removal of *Calanus* species from the surface communities increases the strength of CCS response to temperature and temperature seasonality. Seasonal changes promote changes within the activity and metabolism of species, as resource availability changes, thus promoting compensating life history strategies such as overwintering at depth (Clarke 1993, Hind et al. 2000). Seasonality also influences food and nutrients available to zooplankton and is therefore an important driver of the copepod community body size distribution. The seasonal body size changes we recorded could indirectly highlight resource poor and rich periods throughout the year.

Life history tradeoffs appear to influence the latitudinal-size clines in copepods. Larger copepods are able to survive at higher latitudes in colder temperatures, as they alter markedly their vertical distribution on a seasonal basis. When food becomes scarce, some larger species overwinter at depth, which likely reduces their mortality and metabolic rates. Their large sizes may both allow for storage of greater lipid reserves (Jónasdóttir et al. 2015) and allow lower mass-specific metabolic rates, hence allowing fasting over winter. In contrast, smaller copepods do not have the appropriate metabolism for such an overwintering strategy. *C. hyperboreus*, which can reach high abundance at northern latitudes, had a very weak effect on the relationships between CCS, SST and thermal seasonality. In contrast, these relationships were strongly influenced by a group of species that share the same life history characteristics. These life history differences between large and small copepods sustain the seasonal variation in maximum and minimum copepod community size, regardless of a rather invariant annual mean size. The relationship between CCS and SST is not simply linear (Fig. 3). The sharp increase in body size and lack of conformity at temperatures $<5^{\circ}\text{C}$, could arise from temperature change being a potential cue for the vertical migration of the overwintering strategy in *Calanus* species (Fig. 3). A reduction in food availability and developmental rate has been suggested as the main prerequisite for the onset of overwintering at depth and its duration (Hind et al. 2000). We know that vital rates are influenced by body size and temperature in ectotherms (Atkinson 1994), thus a temperature cue for overwintering is plausible yet unsupported in the literature. Phenological shifts associated with climate warming have been recorded in marine phytoplankton, a main food source for the copepods (Thackeray et al. 2010). The reduction in CCS over time could also result from a phenological mismatch between seasonal phytoplankton blooms and the *Calanus* species cue for overwintering at depth. However, the role of nutrients and phytoplankton in shaping the physiology and ecology of zooplankton could not be directly tested here due to the lack of comparable data.

Oxygen limitation may be another driver of body size change across latitude, possibly affecting the observed relationship between CCS and SST. Metabolic rates tend to increase markedly in warmer environments, yet the availability of oxygen needed to fuel aerobic metabolism does not increase as markedly in warmer water (Verberk et al. 2011, Forster et al. 2012). Under oxygen limitation, smaller sizes may be optimal, with earlier maturation and shorter life spans (Atkinson et al. 2003). Laboratory experiments on copepods, gastropods and amphipods show that reduced oxygen availability restricts growth rates and body size (Marshall and Orr 1955, Wu and Or 2005, Liu et al. 2011). Seasonal variability in temperature may also induce variation in oxygen availability and metabolic demand. Oxygen is less likely limiting at colder temperatures, therefore may be less influential for larger body size at higher latitudes (Verberk et al. 2016). Dissolved oxygen concentration has been decreasing across

the North Atlantic surface waters since the 1950s (Stendardo and Gruber 2012). The availability and metabolic demand for oxygen and how these both relate differently to temperature, may therefore have contributed to the observed latitudinal-size clines in copepods.

The differences in community size structure with and without *Calanus* species partially supports the ‘resource availability hypothesis’, in that when resources are scarcer over winter months, the large sized *Calanus* species overwinters at depth. High food availability likely promotes higher abundances of small copepods at lower, warmer latitudes, as smaller species that mature earlier have a competitive advantage over larger species that mature later (Speirs et al. 2006, Beaugrand et al. 2014). In areas of seasonal food scarcity, the *Calanus* species occupy the upper limits of CCS, such as between 40°N and 50°N and $>67^{\circ}\text{N}$, they can survive periods of resource shortage. Once *Calanus* species are removed from the analysis, only a small number of medium-sized species remain at higher latitudes, suggesting that the environment $>67^{\circ}\text{N}$ does not support high body size variation, in particular smaller sized species which are physiologically less capable of overwintering. We suggest that a reduced food availability might limit the abundances of smaller-sized copepods at higher latitudes, whereas low temperature relates to larger sized-species, which can cope with lack of resource during winter. However, we have not directly measured food availability, and this mechanism remains to be tested directly.

The influence of temperature on the distribution and body size structure of copepod communities across large spatiotemporal scales is profound, and highlights the potential for major food web alterations due to climate warming (Blanckenhorn 2000, Saunders et al. 2018). Moreover, the changes to copepod community sizes have implications for carbon export and supply of a range of biologically-derived elements to ocean depths (Beaugrand et al. 2010, Jónasdóttir et al. 2015). The North Atlantic Ocean contributes 10–25% to the global biological carbon pump (Sanders et al. 2014), but smaller copepods contribute less to the sinking of carbon into deeper waters, due to their higher mass-specific respiration rate, lower carbon mass and slower sinking speeds (Beaugrand et al. 2010, Jónasdóttir et al. 2015). The implications of body size changes within entire communities are not fully understood, but trophic interactions and biogeochemical processes are well known to be size dependent in aquatic systems (Beaugrand et al. 2010, DeLong et al. 2015). Further focus on the macroscale distribution of traits and life history strategies is essential for more accurate forecasts of community structure, dynamics and ecosystem function under future climate warming.

Data availability statement

The continuous plankton recorder data is available upon data request from the Sir Alister Hardy Foundation for Ocean Science (www.sahfos.ac.uk/). Species list and specific copepod body sizes is available in the Supplementary material.

Acknowledgements – Funding – LEE was funded by London Natural Environment Research Council Doctoral Training Partnership studentship (NE/L002485/1). PK gratefully acknowledges funding from the Royal Society (grant no. NAF/R2/180791).

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Supplementary material (available online as Appendix ecog-04631 at <www.ecography.org/appendix/eco-04631>). Appendix 1.