

Temperature-mediated changes in zooplankton body size:

large scale temporal and spatial analysis

Short Running Title: Latitudinal size clines under climate warming

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ABSTRACT

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.

INTRODUCTION

Body size relates to the fitness, ecology and physiology of organisms, and is considered a master trait (Barton *et al.*, 2013; Brown *et al.*, 2004). Ectotherm body sizes change across time and space following changes in environmental conditions (Angilletta *et al.*, 2004; Kingsolver & 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 (Brun *et al.*, 2016a; Violle *et al.*, 2014). 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 (Brun *et al.*, 2016a; Edwards & Richardson, 2004; Kratina *et al.*, 2014). 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 & 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 <math><15^\circ</math> of latitude) or short time periods (<math><10</math> years) (Beaugrand *et al.*, 2010; Brun *et al.*, 2016b; Chiba *et al.*, 2015), 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 & 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 & 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 (Forster *et al.*, 2012; Atkinson *et al.*, 2006). 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 *et al.*, 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 trade-offs (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 trade-offs 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 (Blackburn *et al.*, 1999; Geist, 1987). 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: (i) Establish whether the copepod community in the North Atlantic follows Bergmann's rule; (ii) Examine whether *Calanus* species promote the overall community latitudinal-size cline with their life history trade-offs (i.e. overwintering at depth); (iii) Describe the seasonal changes in copepod community size, and; (iv) 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 10m and speed below 10 knots (Reid *et al.*, 2003). The spatial distribution of these data is available in Supplementary Fig. 1. 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 Table 1). The copepods in this study spanned a size range from 1.3 mm (*Oculosetella gracilis*) to 10 mm (*Paraeuchaeta 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 x 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:

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

Females were chosen to represent species body size as this sex numerically dominates populations for many copepods (Chiba *et al.*, 2015; Rombouts *et al.*, 2009). 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: (i) Latitude, (ii) Longitude, (iii) *CCS*, (iv) SST (v) thermal seasonality and (vi) 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 x 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 & 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 $1^{\circ}\times 1^{\circ}$ grid that contained at least five data points. PCA was performed on the *CCS* and *SST* values per $1^{\circ}\times 1^{\circ}$ 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, 2003, 2016) and the pre-analysis of residuals did not indicate spatial autocorrelation (see Supplementary Material Fig. 3). 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 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 Fig. 2 a, b). *Calanus* species appeared to strengthen the latitudinal-size cline at the upper limits of *CCS* at higher latitudes ($>68^\circ\text{N}$) and at mid-latitudes ($35\text{--}50^\circ\text{N}$) (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 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 (Figs. 4 a, 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 (Angilletta *et al.*, 2004; Belk & Houston, 2002; Sommer *et al.*, 2016). However, quantitative test of latitudinal size clines 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 R² 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 (Hind *et al.*, 2000; Marshall & Orr, 1955). 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 *Calanus helgolandicus*, has been increasing over time (Fromentin and Planque, 1996), a larger species, *Calanus finmarchicus*, has been declining (Fromentin and Planque, 1996), and these

changes seem to be linked to their thermal niches (Helaouet 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 trade-offs 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 (Forster *et al.*, 2012; Verberk *et al.*, 2011). 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 (Liu *et al.*, 2011; Marshall & Orr, 1955; Wu & Or, 2005). 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 (Beaugrand *et al.*, 2014; Speirs *et al.*, 2006). In areas of seasonal food scarcity, the *Calanus* species occupy the upper limits of CCS, such as between 40 °N to 50 °N and >67°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°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 (Saunders *et al.*, 2018; Blanckenhorn, 2000). 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 ACCESSIBILITY

The Continuous Plankton Recorder data is available upon data request from the Sir Alister Hardy Foundation for Ocean Science (<https://www.sahfos.ac.uk/>). Species list and specific copepod body sizes is available in the supplementary material.

REFERENCES

- Angilletta, M. J. et al. 2004. Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life history puzzle. - *Integrative Computational Biology* **509**: 498–509.
- Atkinson, D. 1994. Temperature and organism size - A biological law for ectotherms? - *Advances in Ecological Research* **25**: 58.
- Atkinson, D. et al. 2003. Protists decrease in size linearly with temperature: ca. 2.5% C⁻¹. - *Proceedings of the Royal Society B: Biological Sciences* **270**: 2605–2611.
- Atkinson, D. et al. 2006. From cells to colonies: At what levels of body organization does the “temperature-size rule” apply? - *Evolution and Development* **8**:202–214.
- Barton, A. D. et al. 2013. The biogeography of marine plankton traits. - *Ecology Letters*. **16**: 522–534.
- Batten, S. et al. 2003. CPR sampling: the technical background, materials and methods, consistency and comparability. - *Progress in Oceanography* **58**: 193–215.
- Beaugrand, G. 2005. Monitoring pelagic ecosystems using plankton indicators. - *ICES Journal of Marine Science* **62**: 333–338.
- Beaugrand, G. 2009. Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. - *Deep-Sea Research Part II: Topical Studies in Oceanography* **56**:656–673.
- Beaugrand, G. et al. 2003. Plankton effect on cod recruitment in the North Sea. - *Nature* **426**: 661–664.
- Beaugrand, G. et al. 2002. Spatial dependence of calanoid copepod diversity in the North Atlantic Ocean. - *Marine Ecology Progress Series* **232**: 197-211.
- Beaugrand, G. et al. 2010. Climate, plankton and cod. - *Global Change Biology* **16**: 1268-1280.
- Beaugrand, G. et al. 2010. Marine biodiversity, ecosystem functioning, and carbon cycles. - *Proceedings of the National Academy of Sciences*. **107**: 10120–10124.

- Beaugrand, G. et al. 2014. Marine biological shifts and climate. - *Proceedings of the Royal Society B: Biological Sciences* **281**: 20133350–20133350.
- Beaugrand, G. et al. 2001. Geographical distribution and seasonal and diel changes in the diversity of calanoid copepods in the North Atlantic and North Sea. - *Marine Ecology Progress Series* **219**: 189–203.
- Beaugrand, G. et al. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. - *Global Change Biology* **9**: 801–817.
- Beaugrand, G. et al. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. - *Science* **296**: 1692–1694.
- Belk, M. C. et al. 2002. Notes and comments Bergmann's rule in ectotherms : A test using freshwater fishes. - *The American Naturalist* **160**: 803–808.
- Bergmann, K. G. L. C. 1847. Über die Verhältnisse der wärmeökonomie der Thiere zu ihrer Grösse. - *Göttinger Studien* **3**: 595–708.
- Berke, S. K. et al. 2013. Beyond Bergmann's rule: size–latitude relationships in marine Bivalvia world-wide. - *Global Ecology and Biogeography* **22**:173-183.
- Blackburn, T. M. et al. 1999. Geographic gradients in body size: A clarification of Bergmann's rule. - *Diversity and Distributions* **5**: 165–174.
- Blanckenhorn, W. U. 2000. The evolution of body size: What keeps organisms small? - *The Quarterly Review of Biology* **75**: 385–407.
- Boersma, M. et al. 2016. Projecting effects of climate change on marine systems: is the mean all that matters? - *Proceedings of the Royal Society B: Biological Sciences* **283**: 20152274.
- Brown, J. H. et al. 2004. Toward a metabolic theory of ecology. - *Ecology* **85**: 1771–1789.
- Brun, P. et al. 2016a. The predictive skill of species distribution models for plankton in a changing climate. - *Global Change Biology* **22**: 3170–3181.

- Brun, P. et al. 2016b. Trait biogeography of marine copepods – an analysis across scales. - *Ecology Letters* **19**: 1403-1413.
- Chiba, S. et al. 2015. Temperature and zooplankton size structure : climate control and basin-scale comparison in the North Pacific. - *Ecology and Evolution* **5**: 1–11.
- Daufresne, M. et al. 2009. Global warming benefits the small in aquatic ecosystems. - *Proceedings of the National Academy of Sciences of the United States of America* **106**: 12788-12793.
- DeLong, J. P. et al. 2015. The body size dependence of trophic cascades. - *The American Naturalist* **185**: 354-366.
- Edwards, M. et al. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. - *Nature* **430**: 881–884.
- Falkowski, P. G. 1994. The role of phytoplankton photosynthesis in global biogeochemical cycles. - *Photosynthesis Research* **39**: 235–258.
- Forster, J. et al. 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. - *Proceedings of the National Academy of Sciences of the United States of America* **109**: 19310–4.
- Fromentin, J.-M. et al. 1996. Calanus and environment in the eastern North Atlantic. 2. Role of the North Atlantic Oscillation on *Calanus finmarchicus* and *C. helgolandicus*. - *Marine Ecology Progress Series* **134**: 11–118.
- Geist, V. 1987. Bergmann's rule is invalid. - *Canadian Journal of Zoology* **65**: 1035–1038.
- Gilbert, B. et al. 2014. A bioenergetic framework for the temperature dependence of trophic interactions *Ecology Letters*. **17**: 902-914.
- Gillooly, J. F. et al. 2001. Effects of size and temperature on metabolic rate. - *Science* **293**: 2248-2251.
- Gliwicz, Z. M. 1990. Food thresholds and body size in cladocerans. - *Nature* **343**: 638.

- Heath, M. R. et al. 2004. Comparative ecology of over-wintering *Calanus finmarchicus* in the northern North Atlantic, and implications for life-cycle patterns. - *ICES Journal of Marine Science* **61**: 698-708.
- Helaouët, P. et al. 2007. Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. - *Marine Ecology Progress Series* **345**: 147-165.
- Hildrew, A. et al. 2007. *Body Size: the structure and function of aquatic ecosystems*. Cambridge University Press.
- Hind, A. et al. 2000. Overwintering strategies in *Calanus finmarchicus*. - *Marine Ecology Progress Series* **193**: 95–107.
- Horne, C. R. et al. 2015. Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. - *Ecology Letters* **18**: 327–335.
- Jónasdóttir, S. H. et al. 2015. Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. - *Proceedings of the National Academy of Sciences* **112**: 12122–12126.
- Killen, S. S. et al. 2010. The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. - *Ecology letters* **13**: 184-193.
- Kingsolver, J. G. et al. 2008. Size, temperature, and fitness: Three rules. - *Evolutionary Ecology Research* **10**: 251–268.
- Kjørboe, T. et al. 2008. Optimal development time in pelagic copepods. - *Marine Ecology Progress Series* **367**: 15–22.
- Kratina, P. et al. 2014. Human-induced biotic invasions and changes in plankton interaction networks. - *Journal of Applied Ecology* **51**: 1066 – 1074.
- Litchman, E. et al. 2009. Contrasting size evolution in marine and freshwater diatoms. - *Proceedings of the National Academy of Sciences* **106**: 2665-2670.

- Liu, C. C. et al. 2011. Physiological responses of two sublittoral nassariid gastropods to hypoxia. - *Marine Ecology Progress Series* **429**: 75–85.
- Marshall, S. M. et al. 1955. On the biology of *Calanus finmarchicus*. - *Journal of the Marine Biological Association of the United Kingdom* **34**: 495–529.
- Matsuno, K. et al. 2015. Seasonal changes in the population structure of dominant planktonic copepods collected using a sediment trap moored in the western Arctic Ocean. - *Journal of natural history* **49**: 2711-2726.
- Menzel, A. 2002. Phenology: its importance to the global change community. - *Climatic change* **54**:379-385.
- Montgomery, D. C. et al. 2010. *Applied statistics and probability for engineers*. John Wiley & Sons.
- Morán-Ordóñez, A. et al. 2017. Evaluating 318 continental-scale species distribution models over a 60-year prediction horizon: what factors influence the reliability of predictions? - *Global Ecology and Biogeography* **26**: 371–384.
- Morán, X. A. G. et al. 2010. Increasing importance of small phytoplankton in a warming ocean. - *Global Change Biology* **16**: 1137–1144.
- Nunes, G. T. et al. 2017. When Bergmann's rule fails: evidences of environmental selection pressures shaping phenotypic diversification in a widespread seabird. - *Ecography* **40**: 365–375.
- Partridge, L. et al. 1997. Bergmann's rule in ectotherms: Is it adaptive? - *Evolution* **51**: 632–635.
- Peck, L. S. 2002. Ecophysiology of Antarctic marine ectotherms: Limits to life. - *Polar Biology* **25**: 31–40.
- Planque, B. et al. 2000. *Calanus finmarchicus* in the North Atlantic: the year of *Calanus* in the context of interdecadal change. - *ICES Journal of Marine Science* **57**: 1528-1535.
- Purves, D. et al. 2013. Time to model all life on Earth. - *Nature* **493**: 295–297.
- Reid, P. C. et al. 2003. The Continuous Plankton Recorder: concepts and history, from Plankton

- Indicator to undulating recorders. - *Progress in Oceanography* **58**: 117–173.
- Reid, P. C. et al. 2016. Global impacts of the 1980s regime shift. - *Global Change Biology* **22**: 682–703.
- Richardson, A. J. et al. 2006. Using continuous plankton recorder data. - *Progress in Oceanography* **68**: 27–74.
- Roemmich, D. et al. 1995. Climatic warming and the decline of zooplankton in the California Current. - *Science* **267**: 1324–1326.
- Rombouts, I. et al. 2009. Global latitudinal variations in marine copepod diversity and environmental factors. - *Proceedings of the Royal Society B: Biological Sciences* **276**: 3053–3062.
- Sanders, R. et al. 2014. The Biological Carbon Pump in the North Atlantic. - *Progress in Oceanography* **129**: 200–218.
- Saunders, R.A et al. 2018. Southern Ocean mesopelagic fish comply with Bergmann’s Rule. - *The American Naturalist* **191**: 343-351.
- Sommer, U. et al. 2016. Do marine phytoplankton follow Bergmann’s rule sensu lato? - *Biological Reviews* **92**: 1011–1026.
- Speirs, D. C. et al. 2006. Ocean-scale modelling of the distribution, abundance, and seasonal dynamics of the copepod *Calanus finmarchicus*. - *Marine Ecology Progress Series* **313**: 173–192.
- Stendardo, I. et al. 2012. Oxygen trends over five decades in the North Atlantic. - *Journal of Geophysical Research: Oceans* **117**: C11.
- Stocker, T. (Ed.). (2014). *Climate change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.
- Thackeray, S. J. et al. 2010. Trophic level asynchrony in rates of phenological change for marine,

- freshwater and terrestrial environments. - *Global Change Biology* **16**: 3304-3313.
- Torres-Romero, E. J. et al. 2016. Bergmann's rule in the oceans? Temperature strongly correlates with global interspecific patterns of body size in marine mammals. - *Global Ecology and Biogeography* **25**: 1206–1215.
- Turner, J. T. 2004. The importance of small pelagic planktonic copepods and their role in pelagic marine food webs. - *Zoological Studies* **43**: 255–266.
- Valenzuela-Sánchez, A. et al. 2015. Geographic body size variation in ectotherms: effects of seasonality on an anuran from the southern temperate forest. - *Frontiers in Zoology* **12**: 37.
- Verberk, W. C. et al. 2011. Oxygen supply in aquatic ectotherms: partial pressure and solubility together explain biodiversity and size patterns. - *Ecology* **92**: 1565-1572.
- Verberk, W. C. et al. 2016. Does oxygen limit thermal tolerance in arthropods? A critical review of current evidence. - *Comparative Biochemistry and Physiology -Part A : Molecular and Integrative Physiology* **192**: 64–78.
- Violle, C. et al. 2014. The emergence and promise of functional biogeography. - *Proceedings of the National Academy of Sciences* **111**: 13690–13696.
- Watt, C. et al. 2010. Bergmann's rule; A concept cluster? - *Oikos* **119**: 89–100.
- White, E. P. et al. 2007. Relationships between body size and abundance in ecology. - *Trends in ecology & evolution* **22**: 323-330.
- Wiens, T. 2015. Day Length Calculation. Retrieved May 20, 2017, from <https://uk.mathworks.com/matlabcentral/fileexchange/20390-day-length>
- Woodruff, S. D. et al. 1987. A comprehensive ocean-atmosphere data set. - *Bull. Am. Meteorol. Soc.* **68**: 1239-1250.
- Wu, R. S. S. et al. 2005. Bioenergetics, growth and reproduction of amphipods are affected by moderately low oxygen regimes. - *Marine Ecology Progress Series* **297**: 215–223.

FIGURES

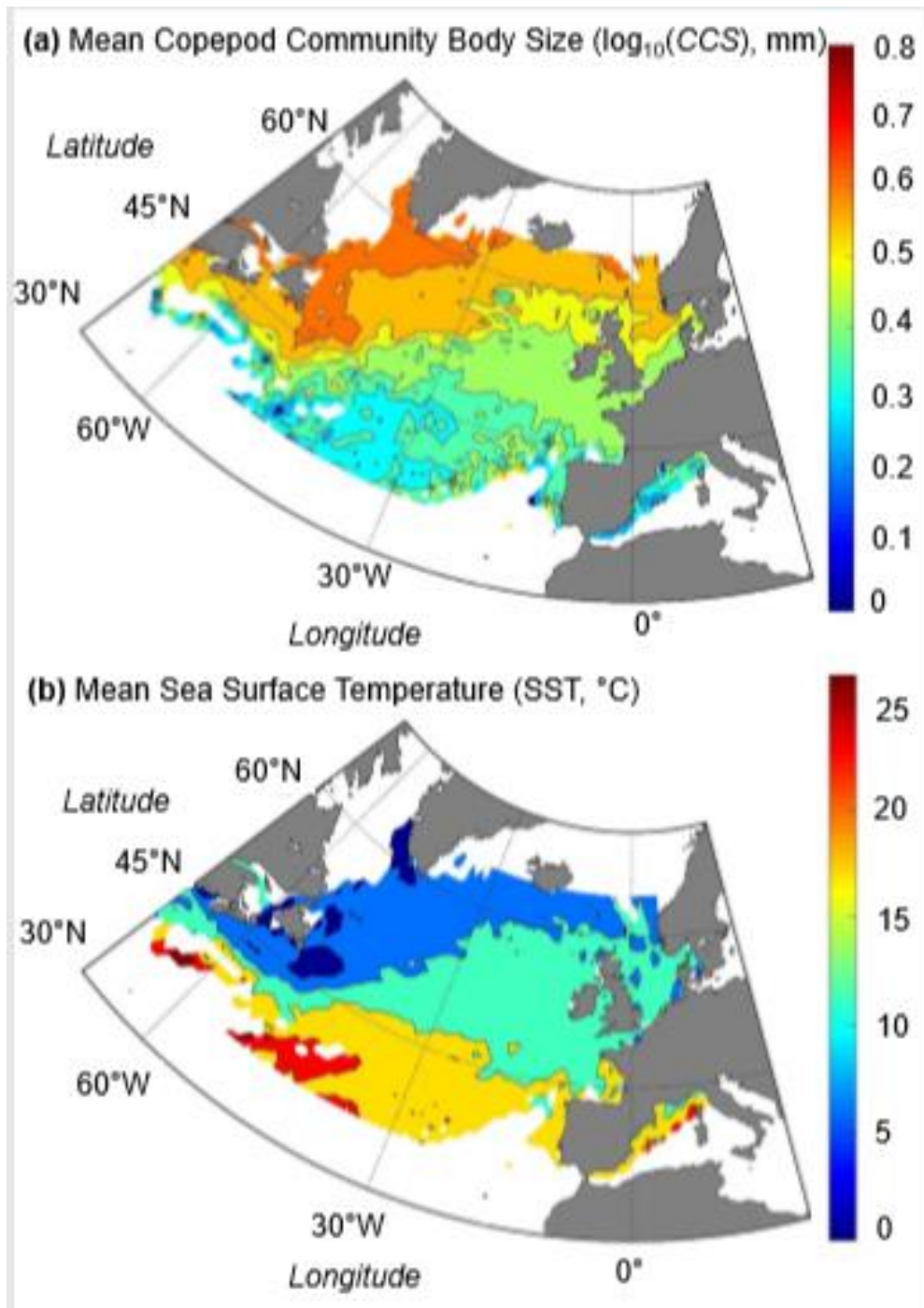


Figure 1: (a) The distribution of copepod community body size $\log_{10}(CCS)$, mm) between 1958 and 2014 across the North Atlantic. A gradient in mean community body size is apparent, with smaller copepod species most common at lower latitudes. (b) Mean sea surface temperature (SST, °C) between 1958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

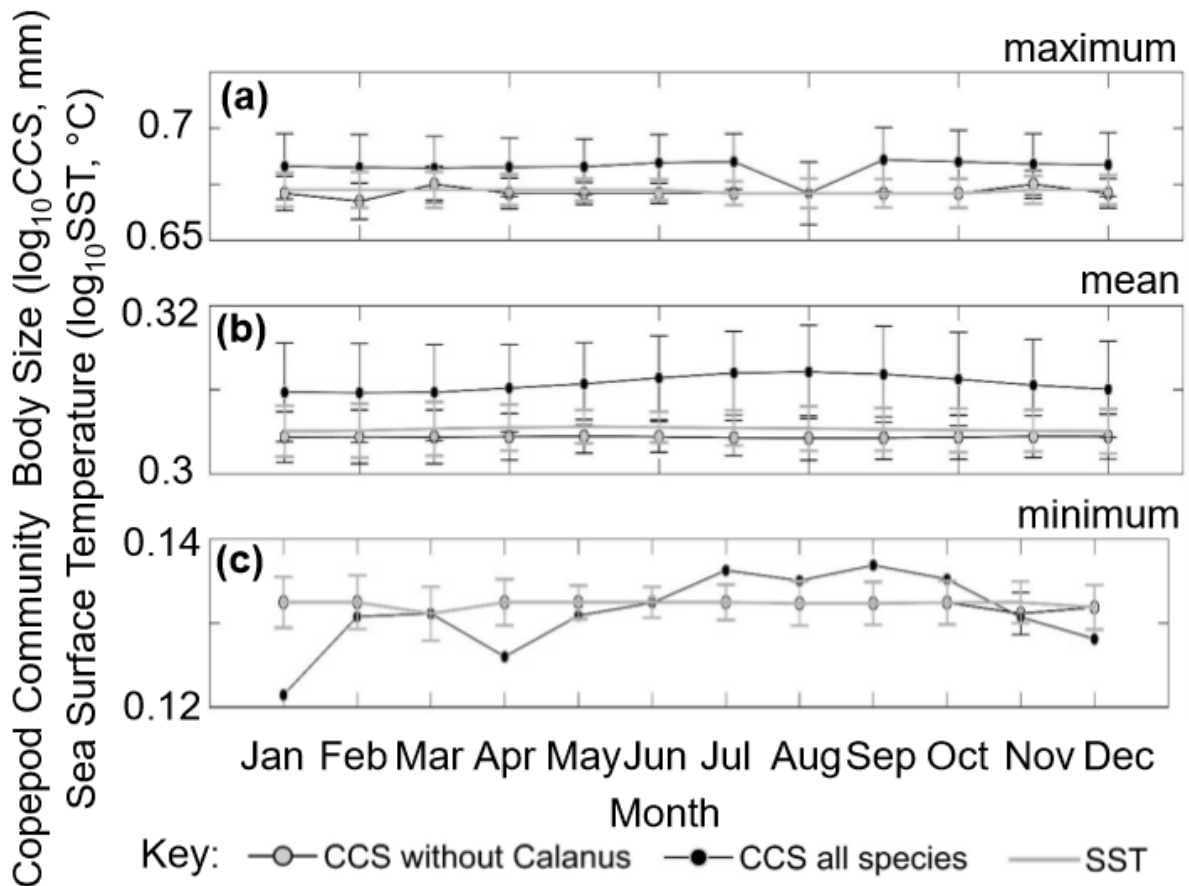


Figure 2: The monthly distribution of (a) maximum, (b) mean, and (c) minimum copepod community body size ($\log_{10} CCS, \text{ mm}$) and sea surface temperature ($\log_{10} SST, ^\circ\text{C}$). All species are illustrated as black data points, whereas data points with *Calanus* species removed are 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, $p < 0.05$, $F = 528.36$, $n = 684$).

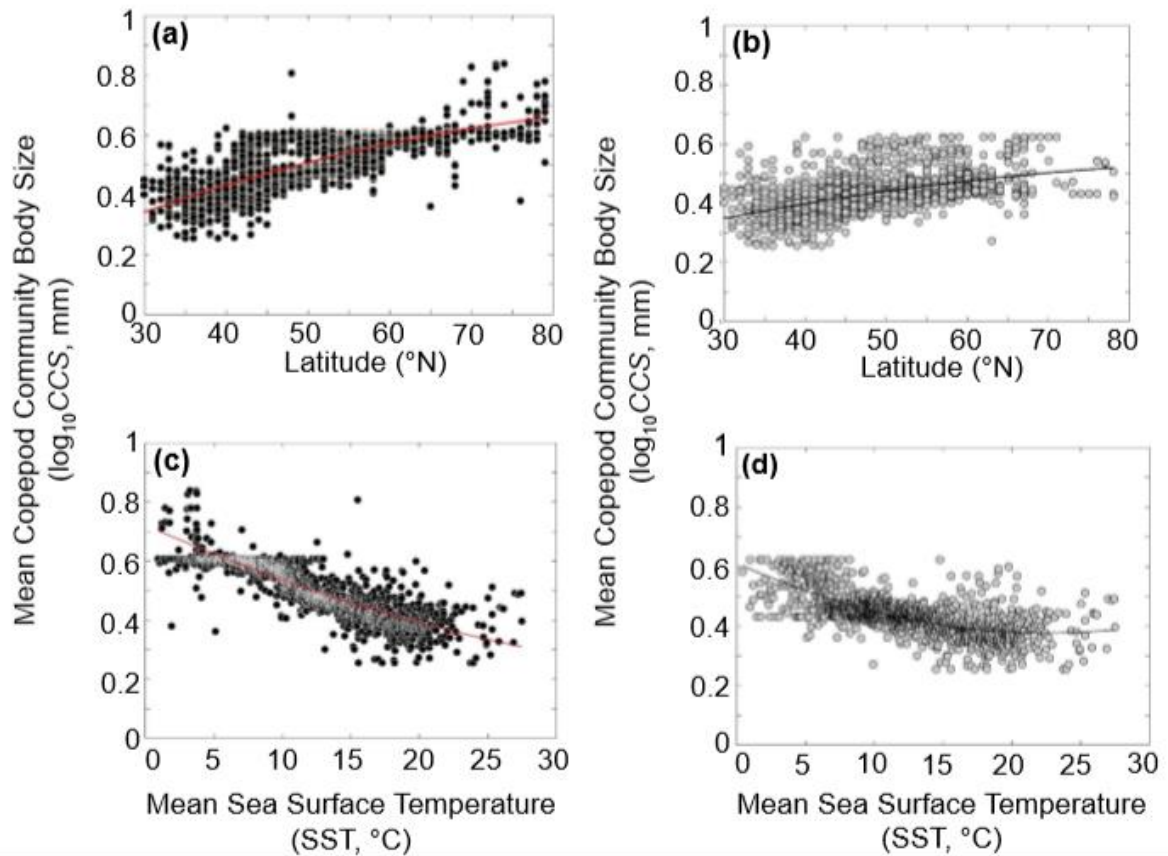


Figure 3: The relationship between copepod community body size and latitude ($^{\circ}\text{N}$) per $1^{\circ}\times 1^{\circ}$ grid cell in the North Atlantic between 1958 and 2014 with (a) all species in black data points and (b) with *Calanus* species removed in grey data points. There is a significant correlation between body size (CCS , mm) and latitude (lat , $^{\circ}\text{N}$) for (a) all species ($R^2 = 0.65$, $p < 0.0001$, $n = 4300$, $\text{CCS} = -0.01\text{lat}^2 + 0.11\text{lat} + 0.5$) 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 $1^{\circ}\times 1^{\circ}$ 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 ($R^2 = 0.8$, $p < 0.0001$, $n = 4300$, $\text{CCS} = 0.01T^2 - 0.1T + 0.5$) and (d) with *Calanus* species removed ($R^2 =$

= 0.6, $p < 0.0001$, $n = 4300$, $CCS = 0.01T^2 - 0.1T + 0.4$). A higher proportion of the variability in CCS is explained by sea surface temperature when *Calanus* species are included.

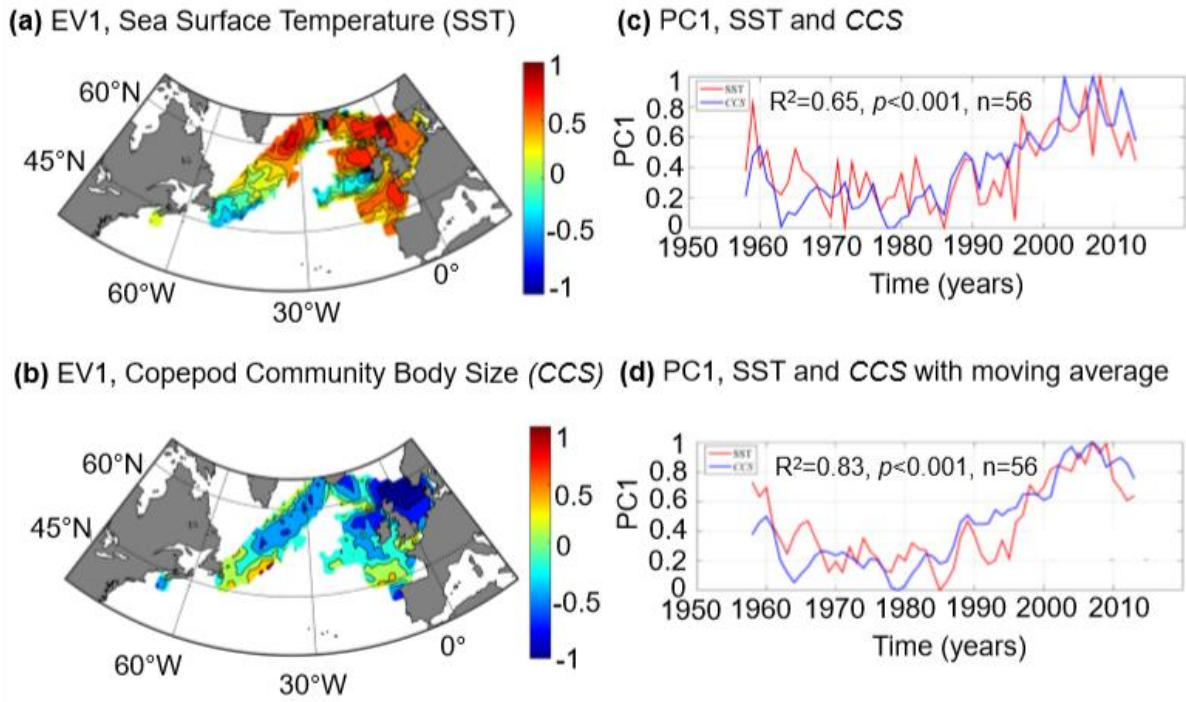


Figure 4: Outputs from Principal Component Analysis on Copepod Community Size (*CCS*) and Sea Surface Temperature (*SST*). **(a)** First normalised eigenvector (*EV1*) for *SST* (51% of the variability). **(b)** First normalised eigenvector (*EV1*) for *CCS* (48% of the variability). **(c)** Correlation 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.