DR. NIALL MCGINTY (Orcid ID : 0000-0002-2505-2531)

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Anthropogenic climate change impacts on copepod trait biogeography

Niall McGinty[1], Andrew D. Barton[2], Nicholas R. Record[3], Zoe V. Finkel[1],
David G Johns[4], Charles A. Stock[5], Andrew J. Irwin[1, 6]

1. Department of Oceanography, Dalhousie University, Canada
2. Scripps Institution of Oceanography and Section of Ecology, Behavior and Evolution, University of California, San Diego, CA 92093-0218, USA
3. Bigelow Laboratory for Ocean Sciences, ME 04544, USA
4. CPR Survey, Marine Biological Association, UK
5. Geophysical Fluid Dynamics Laboratory, National Oceanic and Atmospheric Administration, Princeton University, Princeton, NJ 08540
6. Department of Mathematics and Statistics, Dalhousie University, Canada

Correspondence:
Niall McGinty, nmcginty@mta.ca

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Abstract

Copepods are among the most abundant marine metazoans and form a key link between marine primary producers, higher trophic levels, and carbon sequestration pathways. Climate change is projected to change surface ocean temperature by up to 4°C in the North Atlantic with many associated changes including slowing of the overturning circulation, areas of regional freshening and increased salinity and reductions in nutrients available in the euphotic zone over the next century. These changes will lead to a restructuring of phytoplankton and zooplankton communities with cascading effects throughout the food web. Here we employ observations of copepods, projected changes in ocean climate, and species distribution models to show how climate change may affect the distribution of copepod species in the North Atlantic. On average species move northeast at a rate of 14.1 km dec^{-1}. Species turnover in copepod communities will range from 5-75% with the highest turnover rates concentrated in regions of pronounced temperature increase and decrease. The changes in species range vary according to copepod traits with the largest effects found to occur in the cooling, freshening area in the subpolar North Atlantic south of Greenland and in an area of significant warming along the Scotian shelf. Large diapausing copepods (>2.5mm) which are higher in lipids and a crucial food source for whales, may have an advantage in the cooling waters due to their life history strategy that facilitates their survival in the arctic environment. Carnivorous copepods show a basin wide increase in species richness and show significant habitat area increases when their distribution moves poleward while herbivores see significant habitat area losses. The trait-specific effects highlight the complex consequences of climate change for the marine food web.

Introduction

Pelagic ecosystems have been strongly influenced by climatic change, most noticeably with the increase in ocean temperature (Richardson, 2008), but also through changes in other important environmental conditions such as salinity, mixed-layer depth, and chlorophyll concentration (Curry et al., 2003). Ocean warming has been implicated in changes to the distribution of species across all trophic levels including plankton (Thomas et al., 2012; Barton et al., 2016), marine fish (Simpson et al., 2011; Pinsky et al., 2013) and marine mammals (Hazen et al., 2013; Record et al. 2019). Zooplankton play key roles in the pelagic ecosystem, acting as the link between primary producers and higher-level consumers in marine food webs. As an important food source for many commercial fish species during key stages of their life cycle, changes to zooplankton annual abundance and seasonal dynamics can have significant effects on global fisheries. For example, successful cod recruitment in the North Sea is linked to years with high abundance of key plankton prey species for cod larvae (e.g., *Calanus finmarchicus*) (Beaugrand et al., 2003, Beaugrand and Kirby 2010, Olsen et al., 2011).

Due to the short generation times and fecundity of zooplankton, their populations can rapidly respond (< 1 year) to changes in the marine environment (Richardson, 2008) including to changes induced by anthropogenic pressures (Bedford et al., 2020). As a result, past changes in zooplankton dynamics have been used as ecosystem indicators to inform marine policy and ecosystem management (Racault et al., 2014; McQuatters-Gollop et al., 2015). We focus on copepods as they typically account for between 70-90% of mesozooplankton abundance, are pivotal in many pelagic food webs (Steinberg and Landry, 2017) and are major contributors to carbon sequestration in the deep oceans *via* vertical migration and the lipid pump (Visser et al., 2017), with lower bound estimates around 0.25 Pg C yr^{-1} (Record et al. 2018), and species-specific analyses suggesting that the number is likely even higher (Jónasdóttir et al. 2019). Copepods have been shown to shift their distribution, phenology or both in response to the displacement of their optimal thermal habitat (Edwards and Richardson, 2004; Poloczanska et al., 2013). Changes in timing across trophic levels can vary significantly leading to large scale ecosystem alterations and the break-down of established food webs caused by trophic mismatch (Edwards & Richardson 2004). Previous efforts to model the potential climate impacts on zooplankton abundance and distribution have primarily focussed on modelling of ecologically important copepods, but one drawback of this approach is the challenge of generalizing the analysis of one species to others or whole communities. Here we shift focus from species to three functional traits to assess the functional biogeography of copepods in the North Atlantic. Specifically we consider body size, dietary strategy, and diapause that mediate growth, reproduction and survival (Litchman et al., 2013).

Zooplankton traits including body size, dietary strategy, and diapause are known to structure realized niches of copepods in the present ocean (Brun et al, 2017; Benedetti et al., 2018; McGinty et al., 2018). Body size is considered a master trait for all planktonic organisms as it constrains many other traits including feeding behaviour (Prowe et al., 2018) and diapause (McGinty et al., 2018). Body size has a defined biogeography adhering to Bergmann's temperature-size rule with the larger individuals found in the colder higher latitudes (Brun, et al., 2016; McGinty et al., 2018) and can vary seasonally depending on the community composition (Evans et al., 2019). Dietary strategy appears to have a strong effect on species biogeography with significant niche differentiation of carnivorous copepods that tend to dominate warmer waters with lower chl-*a* biomass and herbivorous copepods which are found in cooler waters with higher chl-*a* biomass (McGinty et al., 2018). Herbivorous strategies also tend to favour species that can adapt to extreme temperature changes and food availability through lipid storing and by employing diapausing strategies (McGinty et al., 2018). The strength of these trait-derived niche-environmental relationships highlights the importance of using traits to anticipate the potential effects of future climate change (Barton et al., 2013). Using a niche characterisation for phytoplankton (Irwin et al., 2012), a basin wide community change and community re-organisation has been projected for the next century with a median northward movement of 12.9 km dec^{-1} (Barton et al., 2016). Changes in phytoplankton communities will affect copepods, likely affecting spatial distribution of herbivores which depend directly on primary producers and carnivores which are secondary consumers. Similarly, biogeographic changes in herbivorous zooplankton will affect phytoplankton communities, although we do not explore that feedback here.

We use species distribution models (SDMs) to identify the relationship between patterns of biogeography for each species and the local environmental conditions (Elith et al., 2006; Elith and Leathwick, 2009). SDMs have revealed taxonomic structure in phytoplankton realised niches (Irwin et al., 2012; Brun et al., 2015) and trait-based differences in the realised niches of zooplankton (McGinty et al., 2018). SDMs have been used to project potential changes future climatic change may have on the biogeographical distribution and movement of species using projected oceanic conditions as the environmental predictors of the future habitat. Individual species projections have shown that poleward movements of up to 23 km yr^{-1} over may occur for *C. finmarchicus* (Beaugrand et al., 2008). A mean poleward shift of 8.7 km dec^{-1} was detected for 14 of the most abundant zooplankton species of the North Atlantic (Villarino et al., 2015) using SDM techniques. Climate projections based on copepod niches have largely been investigated using small collections of species and generally do not consider the potential community responses (e.g., changes in species richness) or trait structure (but see Benedetti et al., 2018 for the Mediterranean).

We quantify projected changes to copepod communities in the North Atlantic over one hundred years between the late 20th and late 21st centuries and categorise these changes using copepod functional traits of body size, dietary mode, and diapause strategy. We develop SDMs for a set of 62 copepod species using observations from the Continuous Plankton Recorder (CPR) collected between 1958 and 2000. Insights into the potential future changes of zooplankton dynamics in the pelagic ecosystem are developed by combining coupled ocean-climate model projections of future ocean conditions with statistical analysis of historical biogeography of zooplankton. Environmental variables used for developing the SDMs are derived from the Geophysical Fluid Dynamics Laboratory's Earth System Model GOLD (ESM2G) under a "business as usual" approach to greenhouse gas emissions (RCP8.5). Environmental change is not expected to be uniform across the North Atlantic, with areas of warming and cooling expected (Bopp et al., 2013). As a consequence, we anticipate hotspots where the greatest changes in copepod community structure are likely to occur and seek to identify the key traits associated with these changes. By focusing on functional traits rather than species we aim to provide a unifying view of the consequences of climate change across all copepods in the North Atlantic linking body size, dietary strategy, and diapause to key ecological and biochemical consequences of food quality, food web structure, and carbon trophic transfer and export efficiency.

Methods

Study area and biotic and abiotic data

Our study region comprised the North Atlantic and shelf sea regions between 35 – 70° N. Species were selected from the Continuous Plankton Recorder (CPR) survey spanning more than 60 years (Richardson et al., 2006). The CPR survey is unrivalled in temporal and spatial coverage, but depth sampling is restricted as the CPR device is towed at ~7 m depth behind ships of opportunity (Richardson, 2006). Most copepod species undergo large diel vertical migrations with larger near-surface abundances found at night than during the day (Hays 2003). Our study aggregates samples across large swathes of space and time (1^{0} and 1 month) combining nearby samples throughout the day ameliorating the problem of surface sampling. The process of diel vertical migration aids in providing a picture of depth-integrated zooplankton communities (Hosie et al., 2003) with surface CPR samples found to correlate with abundance estimates of *C. finmarchicus* down to 100m (Helaouët et al., 2016).

While the use of abundance estimates have been advocated for distribution modelling (Howard et al., 2014), we chose to reduce the data into aggregated 1° monthly grids and convert the species into a presence-only dataset. Abundance data can provide further information on changes within a community, however the processes that govern abundance operate at finer resolutions than those investigated here (Boulangeat et al, 2012). Our interest was in modelling the realised niches of species and identifying the biogeographical distributions a species could maintain given its physiological constraints which can be identified using a presence-absence dataset (Chase and Leibold, 2003). Our approach allowed us to compare the changes of both common and rare species on a similar scale as we focus on logistic probabilities (0-1) of occurrence and biogeographies as opposed to biomass or abundance (Barton et al., 2016). Taxa found in at least 30 of these monthly grids were retained for modelling, resulting in a set of 62 copepod species or genera (Supplementary Table 1). For our analysis, we used seven environmental parameters known to directly indirectly zooplankton biogeography. These variables were (1) Sea Surface Temperature (SST), (2) Sea Surface Salinity (SSS), (3) Mixed Layer Depth (MLD) , (4) Chlorophyll-*a* (Chl-*a*), (5,6) u and v current vectors from the (ESM2G) model (Dunne et al., 2012) and (7) Bathymetric Depth which was taken from the GEBCO 1 arc second resolution dataset (Hall 2006). Temperature affects the physiological and metabolic processes of the individual such that sustained changes to the ocean temperature will lead to changes at the population level (Record et al., 2010). While others can alter the vertical and horizontal transport of an individual (MLD - water column stability; u and v vectors - eddy mediated transport) (Keister et al., 2011). These data were aggregated into the same 1° monthly grids as the CPR to allow for direct matching of the environmental variables according to the location (grids) and time (month) when applicable. We used environmental variables from the GFDL ESM2G model averaged into monthly grid values for both historical (1951 – 2000) and future time periods (2051 – 2100) for training on historical values and for spatial projection of species biogeographies in the future. Full details on data aggregation and model selection can be found in McGinty et al. (2018).

Species distribution models and validation

SDMs were developed for each of the 62 species using multiple model techniques to create an ensemble forecast of species distributions. For this effort we used BIOMOD (Thuillier et al., 2009), which offers a framework to combine the various statistical techniques used in species distribution modelling using the 'biomod2' package in *R* (Thuiller et al., 2016). We chose two machine learning algorithms (random forest - RF and maximum entropy - MaxEnt) and two linear regression (generalised linear models - GLM, generalised additive models - GAM) approaches which cover a large range of model flexibility from linear model relationships (GLM) to highly non-linear (RF). All modelling parameters remained fixed across species to maintain consistency and to prevent model overfitting. Model accuracy was evaluated using the area under the curve (AUC) and the true skill statistic (TSS). A weighted average of the models were generated using BIOMOD for each species where models with the highest AUC and TSS were given the greatest weighting to produce an ensemble model projection for the historical and future periods across the spatial domain of the North Atlantic. We used the ensemble model to generate an estimate of the logistic probability for each species in each 1° cell of the North Atlantic for the historical (1951-2000) and future (2051-2100) periods.

Projected changes in species movement and community organisation

Our analysis of species biogeography and total community characteristics between the historical and future periods followed a similar procedure outlined by Barton et al. (2016) for phytoplankton across the same spatial domain. The species' core biogeographical range was defined using the procedure outlined within BIOMOD, where a cell is considered to be part of a species' core range when the logistic probability of the species being present is above a threshold defined by the TSS for each model. The number of 1° cells above the specified TSS was considered the core range of the species and was converted to an area (km^2) by calculating the grid cell areas as they vary with latitude.

Core range movement was calculated for each species by measuring the changes in the central position for each month between the historical and future periods. The central position was calculated by finding the average location of all grid cells defined within the core range, weighted by the grid cell areas. The central position of each species was calculated for each month of the year and the change in the core position was calculated by finding the difference in the central position for the historical and future periods. An annual measure of median range shift was calculated with the total distance travelled (km), rate of change (km dec^{-1}) and the bearing (-180° to 180°) reported.

The Bray-Curtis similarity index was used to estimate the similarity of the copepod community within each 1^{o} grid cell between the future and historical periods. The estimated logistic probability of a species being present was used to compare the changes within the community. The smaller the Bray-Curtis index the less similar the community is between the two periods indicating a potential change to the copepod community through the gain and loss of the biogeographical range of the constituent species due to the changing environment.

We explored these patterns in more detail by assessing the changes to each species' habitat area and species turnover within a community. We converted the logistic probabilities for each species to a projected presence or absence using probability thresholds defined by maximizing the TSS from each model. The total habitat area for each species was calculated by summing the area associated with each projected presence location in both the historical and future periods. For each grid square we also calculated the species richness, species loss due to local extinction (A), retained species (B) and species gain due to local colonisation (C) between the future and historical periods with the percentage turnover defined as 100 (A+C)/ (A+B+C).

We estimated the timing of the seasonal peak for each species using the monthly logistic probability for each species within each 1° grid. The seasonal peak was calculated as the weighted mean of the month (Jan=1, Feb=2, etc.) and the logistic probability as the weights (Edwards and Richardson, 2004). For each 1° grid, the median seasonal peak for all species was calculated for both the historical and future periods with the difference providing a spatial reference for how timing of the community changes across the region.

Projected changes in trait structuring

Species were classified into trait categories for 1) total body length (0 – 2.4 mm and > 2.5 mm), 2) diapause behavior (diapause, non-diapause) and 3) dietary strategy (Carnivore, Herbivore) which were derived from the comprehensive copepod trait database compiled by Brun et al. (2017). These traits were found to structure present day copepod niches in both the Atlantic and Southern Oceans (McGinty et al., 2018). The mean niche values across each environmental gradient were found by calculating the weighted mean, using the logistic probability as the weight function.We assessed the changes in the logistic probability from historic to future periods within each of the four size categories by calculating the difference in the historical and future median logistic probability of each size class within each 1° grid.

Changes in the distribution of the three trait strategies were examined by calculating the changes in the ratio of trait categories between the historical and future periods. Species were defined as present or absent in each grid cell based on the TSS thresholds of the logistic probabilities derived from the BIOMOD model. Ratios of diapause – non-diapause, small sized (< 2mm) – large sized (> 2.5mm) and carnivore – herbivore species were calculated for both periods. Differences in the ratios between both periods indicate how the spatial trait structure is expected to change over time.

Results

Changes to environment

Mean temperature increases of 1.25 °C are expected across the North Atlantic, with peak temperature increases of almost 4 °C found on the NW Atlantic Shelf in a region ~500 km east of Newfoundland with cooling of similar magnitude expected in the sub polar area south of Greenland. This results in almost 8°C increase in the temperature differential between these regions of the North Atlantic (Fig. 1a). Salinities show a strengthening of the latitudinal salinity gradient with a freshening of the ocean occurring in the subpolar and Arctic regions and increase in surface salinity occurring in the subtropical and tropical regions (S 1b). Mixed layer depth decreases throughout much of the North Atlantic (S 1c). Chl-*a* concentration decreases most in the lower latitudes and increases most significantly in upwelling and subpolar regions (S 1d). The *u* and *v* velocity vectors (that is, East-West and North-South, respectively) show bordering areas of increases and decreases in the mid-Atlantic oriented along the longitudinal and latitudinal gradients (S 1 e, f).

Model performance and niche characteristics

AUC values varied between 0.67 and 0.97 with a mean of 0.86 while TSS values varied between 0.24 and 0.87 with a mean of 0.67. (S 2 a, b). There were no significant differences in the overall performance of each of the four SDM methods averaged across all species. For all species we were able to find at least one model that satisfied our lower limit criteria of an AUC > 0.7 and TSS > 0.5.

Mean niche values for the historic period varied according to trait groups (Table 1). For example, mean SST niches differed between the three trait category groups with herbivorous, diapausing and larger body sized copepods occupying colder niches than their carnivorous, non-diapausing and smaller bodied counterparts. The historical distribution showed differences in the mean historical latitude of the trait groups with diapausing, herbivorous and larger (>2.5 mm) body sized copepods appearing between 4-6° of latitude further north than their opposing counterparts.

Species movements and changes to habitat

The majority of species displayed a net northward movement in their core range with 66% of species moving an average distance of 18.9 km decade^{-1} northward while the southward moving species travelled a distance of 9.1 km decade^{-1}. The greatest movement occurred in species with historical core ranges in the mid-latitudes > 42 N, moving on average 7.2 km decade^{-1} more than species in the tropical and subtropical region (Fig. 2a). Almost 75% of species were projected to move in an eastward trajectory regardless of their movement latitudinally (Fig. 2b). The central position of carnivore habitats moved 0.49 km decade^{-1} faster than herbivores. Carnivores showed an average of ~5% increase in core habitat area compared with a ~5% decrease for herbivores. Diapausing copepods moved 2.2 km decade^{-1} faster than non-diapausing copepods with a ~5% decrease in core habitat area. Differences in the core range movement and changes in core habitat area were minimal for both body size categories. Differences in species movement between the two groups were less than 0.2 km decade^{-1} while both size categories showed < 1% increase in core habitat area (Table 1). Examining the species-specific changes in habitat for both trait groups we found that 75% of all carnivorous species showed a net positive increase in habitat area in contrast to 44% of herbivorous copepods. There was a significant positive relationship between the change in habitat and the change of the central latitude position for carnivores while a contrasting significant negative relationship was found for herbivores (Fig. 3a).

Phenology

The mean time of peak prevalence (phenology) of the copepod community varied between May and July across the North Atlantic (Fig. 4). Historically, the earliest timing occurred in the North Sea and mid-Atlantic with the latest peak time occurring in an area off Iceland's south coast. South of 40° N we found that peak timing was expected to occur marginally earlier in the future. North of 40° N we found an east-west pattern with peak time occurring later along the coast and in the Labrador Sea by an average of 0.2 months (~ 6 days) and in the mid-Atlantic peak time occurs earlier by an average of 0.35 months (~10 days).

Changes in community similarity

Overall, community similarity between the historical and future periods was high, implying that for many regions the change in community structure was not dramatic (Fig. 1b). However, for the NW Atlantic shelf and Atlantic subpolar regions, large changes in community structure were projected. The projected changes in Bray-Curtis similaritywere linearly related to the projected changes in the environment, particularly SST. The greater the magnitude in temperature change expected the less similar two communities become (Fig. 1c). While there was an immediate decline in Bray-Curtis similarity for temperature differences < 0°C, there was a plateau in Bray-Curtis similarity for temperature increases up to 1.7°C. The patterns in Bray-Curtis similarity were reflected in the patterns of species richness change with significant loss (~48%) experienced in the subpolar region and increases >50% in species richness of the NW Atlantic Shelf (Fig. 1d). While much of the tropical and subtropical areas showed widespread loss of species richness ~10%, areas south of Iceland and in the North Sea showed further areas of significant species richness increase that was not apparent with the Bray-Curtis similarity distribution. Similar patterns were observed for species turnover, with turnover rates of up to 80% found in the same areas with the greatest change in Bray-Curtis similarity (S Fig. 3).

Changes in trait distribution

When comparing between historic and future conditions, the percentage of diapause species increased by almost 20% in the "cold spot" location to the south of Greenland while decreases of 5-10% are found on both sides of the cold spot increase and centred along the Scotian shelf and off the coast of Norway (Fig. 5 a, b). Carnivorous copepods showed a basin-wide increase in species number of 8.6% and increased by up to 20% in the subtropical latitudes. Herbivorous copepods showed restricted, regional increases in species numbers with the largest increases shown to occur between Labrador and Greenland (Fig. 5 c, d). The change in the ratio of the small and large (> 2.5mm) individuals show a similar pattern shown for diapause species with >20% increase in large bodied individuals in the "cold spot" (Fig. 5 e, f). In the Arctic region while diapause species percentage decreased, the number of large bodied species remained unchanged..

Discussion

Our analysis demonstrated considerable changes to the North Atlantic copepod community due to projected climate change stemming from a business as usual approach to carbon emissions. Individual species trajectories show predominantly north-eastward movement in their central habitat location with the fastest trajectories displayed by species occupying the mid-latitude areas. These changes manifest themselves at the community level with basin-wide shifts in community composition and changes in species diversity and turnover. The implications of the changing biogeographic patterns for ecosystem functioning were explored by combining information on each species functional trait. Diapausing copepods and larger bodied copepods may tend to increase in the Arctic and sub-Arctic while smaller bodied species will increase across the sub-tropics. One of the most notable findings is the contrasting responses of carnivorous and herbivorous copepods to the projected poleward shifts in species habitat. We find basin-wide increases in the number of carnivore species within a community, with carnivores increasing in overall habitat area as they move northward while herbivores will notably decrease. The anticipated changes to the oceanic conditions within the next century are expected benefit carnivorous copepods at the expense of herbivores which has the potential to alter trophic links and ecosystem functioning for the North Atlantic.

Shifts in species distribution

The rates of zooplankton species shift observed here are broadly similar to the historical poleward shifts observed by Villarino et al. (2015) for 15 copepod species in the North Atlantic (Villarino - 8.7 km dec^{-1} ; this study – 10.8 km dec^{-1}). A comparison between the rates of change in central position measured across both studies show strong correlation ($r=0.66$, $p < 0.001$) when the two Arctic species *C. glacialis* and *C. hyperboreus* are removed. The discrepancy is likely in response to a significant cooling in the sub polar gyreregion, which is thought to be due to a decline in the overturning circulation of the subpolar gyre (Yang et al., 2016). As a result, we propose that Arctic species may counterintuitively shift southward in response to a potential thermal refuge instead of continuing tracking conditions northward. The historical rate of change for the subarctic species *C. finmarchicus* was found to be moving northward at a rate of up to ~111 km decade^{-1} (Helouet and Beaugrand, 2009). With the projected cooling expected, our study finds a much less dramatic rate of direction change of -0.37 km decade^{-1}.

Historical changes in zooplankton biogeographies over the last 50-75 years often show much faster rates of change than our results that compare the average historical distribution with a projected distribution derived from the anticipated changes to the marine environment. Collective estimates of marine range shifts observed rates varying between 1.4 – 28 km decade^{-1} for fish and invertebrates (Cheung et al., 2009) while a meta-analysis of 129 marine species show an average rate of 19 km year $^{-1}$ (Sorte et al., 2010). Copepods are expected to move northward at a similar rate as phytoplankton. A study of the future changes on the North Atlantic phytoplankton community showed that species move northward at a rate of 12.9 km dec^{-1}

(Barton et al., 2016) which is similar to the 10.8 km dec^{-1} demonstrated in our study for copepods. However, phytoplankton may move eastward at a faster rate (phytoplankton - 42.7 km dec^{-1} ; copepods - 21.3 km dec^{-1}), possibly leading to increasing mismatches in the distribution of the two groups (Asch et al., 2019). Even the presence of small mismatches between phytoplankton-copepods, in terms of abundance, distribution, or timing can have large effects on ecosystem functioning (Thackeray, 2012). The expected cooling of the subpolar region during this time rapidly slows and in some cases reverses the predictions of rapid poleward movement that has been observed historically.

Other metrics of species movement have been reported for species, such as the distributional ranges of a species distribution known as the leading (or trailing) edge (Poloczanska et al., 2013). These are usually seen as more dynamic with species movements tending to move much faster than the distributional centre due to an increased adaptability of individuals at the environmental extremes (Vejo et al., 2011). Several plankton species have shown that individuals at the extreme thermal ranges undergo local adaptation to the environment which may not be representative of the whole population (Sasaki & Dam, 2019) The choice of the distributional centre as a metric for species distribution is expected to give a more conservative and robust estimate of any changes to a species biogeography. Nevertheless it is important to acknowledge the broader definitions of a species range as several meta-analytical studies that focused on edge changes are influential and frequently cited (Yohe and Parmesan, 2002, Poloczanska et al., 2013). For example, Poloczanska et al. (2013) found that zooplankton had some of the fastest leading edge expansions of 142.1 km decade^{-1} which is an order of magnitude larger than any measured changes of the distributional centre.

Phenology

Regional studies of copepod phenology have demonstrated a consistent shift toward earlier bloom times in response to warming ocean temperatures (Greve et al., 2004; Mackas and Beaugrand, 2010). The change in the distribution and prevalence of diapausing copepods may have an effect on the changes observed in the phenological landscape of the North Atlantic. In our projections, the mean timing of copepod seasonal peaks changes by up to ±0.5 months, appearing later in the higher latitudes and earlier in the subtropics suggesting that it may be too simple to state that copepod phenology shifts earlier in a warming climate. Based on the geographical patterns, the phenological changes appear to integrate elements of the effects based on diapause strategy, diet preference, and body size. Some of the largest temperature increases coincide with species occurring both earlier and later in the season. At ocean basin scales, we find that the link between phenology and the changing environment is obscured due to the regional variability of individual species responses to environmental conditions (McGinty et al., 2011). Modelling studies have shown the importance of diapause timing to the phenology of several species (Maps et al., 2012) which can produce knock-on ecological effects to non-diapause species in the ecosystem such as introducing competition with species that traditionally did not overlap in their timing (Sullivan et al., 2007). Temperature niches vary according to dietary preference, so we anticipate temperature changes will have differential effects on the phenology of herbivores and carnivores (McGinty et al 2018). Phenological changes will likely cascade through trophic levels and create timing mismatches between copepods and developmental stages of several commercially important fish species (Mollman et al., 2005; Paulsen et al., 2017, Staudinger et al., 2019). Our findings suggest that climate-mediated changes in zooplankton phenology may be more complicated than previously imagined and involved interactions across multiple traits that future research should investigate further.

Changes in community similarity and trait distribution

We identify several key areas where the greatest change in the communities is likely to occur. As the results are not sensitive to changes to abundance, the results emphasize areas where a high number of species have gained or lost their fundamental habitat niche. The greatest change in Bray-Curtis similarity tends to occur in areas with the greatest environmental change, however, changes in species diversity reveal a more varied pattern of change across the whole North Atlantic. When viewed in the context of the underlying environment conditions we find that these changes occur when mean ocean temperatures vary around 9-12℃. This has been identified a critical thermal boundary for copepods in the North Atlantic and is identified as transitional region between temperate and sub-Arctic biomes (Beaugrand et al., 2008, Beaugrand and Kirby, 2018).

Model projections anticipate that body sizes will shrink among lower trophic level groups (Cheung et al., 2013), particularly in the mid-latitude regions, but with little change in the Arctic

(Lefort et al., 2015). Similarly, this phenomenon has also been detected in field studies (Daufresne et al, 2009). Our results suggest that larger species will be lost at the expense of the smaller sized species, particularly in the tropical and subtropical areas. However, between 50-60º N there is an increase in the presence of large-sized species in the subpolar region where significant cooling is expected. Increasing temperatures impose greater metabolic demands on an individual with greater pressure placed on larger individuals to increase energy intake to maintain a suitable basal or active metabolic rate (Claireaux and Lefrancois, 2007). The community response to increasing temperatures appears to be either a reduction in the overall length (Garzke et al., 2015) or an overall reduction in the larger species from an area. As a result of the warmer temperatures and decreases in the larger species, there is the potential to alter the food web structure and the potential of less energy and carbon transfer between trophic levels (Lewandowska and Sommer, 2012).

We project that as a result of climate-induced changes, the North Atlantic ecosystem will become more favourable to carnivorous copepods in the next century while in contrast the prevelence of herbivorous copepods will diminish. In general we find that the probability of presence of carnivore species will tend to increase among copepod communities throughout much of the North Atlantic with the exception of the cooling region which shows a shift towards further herbivore dominance. Most significantly, we find that the poleward movement in a species biogeographical distribution will lead to increases in the overall habitat area for carnivores and decreases for herbivores. Over larger scales, it has been demonstrated that on average carnivorous copepods tend to have niches that in areas with higher temperatures and lower chlorophyll-*a* biomass in contrast to herbivorous copepods (McGinty et al., 2018). Recent evidence has also shown that despite a decline in overall copepod abundance in UK shelf waters due to phytoplankton community changes, several carnivorous copepods have been shown to be increasing (Schmidt et al., 2020). Herbivore-dominated copepod communities are typically simpler with more efficient carbon flow between primary productivity to the higher trophic levels (Castellani et al. 2008). Carnivore dominated systems often occur in tropical and oligotrophic regions where trophic interactions are more complex and tend to be dominated by top-down as opposed to bottom-up processes (Hébert et al., 2017). The projected increases in ocean temperature point to a decrease in the appearance of the largest-sized copepod species and an overall shift in the community to copepods with a preferred carnivorous dietary strategy.

Together with the shifts in phenology and distribution of diapausing species, there will be significant changes to the functional biogeography of the copepod community within the next century. Combined with a loss in accessible energy through a reduction in the larger lipid-rich species and effective phytoplankton–copepod food web links, the effects of the copepod community restructuring will undoubtedly reverberate throughout the ecosystem with significant knock-on effects to the upper trophic levels.

Marine management policy has been shifting from a sectoral based to ecosystem based management system in recent decades and for the Northeast Atlantic, this has been driven largely by initiatives outlined by the Marine Strategy Framework Directive (MSFD). Plankton have been outlined as important indicators for pelagic ecosystem health due to their rapid responses to changes in climate change and water quality (Garmendia et al., 2013). Indices built on changing ratios of plankton functional types have been implemented for the North Atlantic region that provide simple measures of ecosystem resilience to anthropogenic pressures (McQuatters-Gollop et al., 2019). Our trait based ratios are designed on a similar framework that can be used as indicators of changes in energy flow (dietary strategy) and foob-web structure (body size)within the pelagic ecosystem.

Caveats

We must note that there are limitations and uncertainties with any projection model. We included many potential environmental predictors that will change in the next century while others were omitted. Ocean acidification is likely to be a major threat for several calcifying planktonic organisms (e.g., pelagic gastropods; *Limacina spp.*). Studies on copepods have demonstrated that ocean acidification is expected to be of minor effect relative to temperature change (Garske et al., 2016) and as a result was not included here.

Studies have repeatedly shown that the prevailing response of copepod communities to changing environmental conditions is to alter their distribution or timing of life history events in line with these changes. However, some evidence has pointed to the potential for some species to adapt to localized conditions with a rapid genetic response (Dam, 2013). Adaptations of life history traits in response to changing temperatures and thermal extremes have been found for estuarine and coastal copepod species across their geographical ranges (Lonsdale and Levinton, 1985, Willet, 2010). With regards to more widely distributed species, adaptation to local conditions have been found for isolated popaulations of *C. helgolandicus* in the Mediterraanean (Yebra et al., 2011), however no variation was found for its congener *C. finmarchicus* across the North Atlantic. Comparing both species in the open ocean, Hinder et al. (2014) found no evidence of thermal adaptation of either species. We assume that while thermal adaptation is possible the more likely results is for zooplankton species to track their thermal niche.

With the changes expected in the distribution of copepod species among the trait groups, it is likely that changing species interactions (i.e. competition, predator-prey relationships) will occur in the future (Dawson and Pearson, 2003). Future studies should attempt to disentangle the effects of competitive interactions in the copepod community. Finally, we note that the CPR survey, while extraordinary in its spatial and temporal extent, takes all its samples from surface waters. As a result, we have only explored the responses in the surface of the ocean and did not consider the potential changes in the vertical distribution or migration behavior of each species in response to changing climate (Pinsky et al., 2013).

Conclusions

Our results demonstrate that the projected environmental changes in the North Atlantic may lead to profound changes to the copepod community in the latter half of this century with significant geographic shifts expected for most species. We use traits to describe the effects of environmental change across many variables to provide descriptions of the effects of climate change for many species. The analysis of whole communities of copepods and analysis of the response according to three key traits (diapause, dietary strategy, and body size) enables robust estimates about the likely changes in copepod biogeography grounded in known physiological mechanisms. The emphasis on traits

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	Niche values					**Species Range**			
	SST	**SSS**	**Chl-*a***	**MLD**	**Bathymetry**	**Area km^2**	**Hist lat**	**Fut/Hist %**	**km dec^{-1}**
				Diapause					
Yes	$11.15^{1.9}$	$32.48^{1.6}$	$0.58^{<0.1}$	$9.17^{2.6}$	$105.2^{18.1}$	6.2×10^{-3}	50.25	-4.97	6.96
No	$15.45^{1.2}$	$34.52^{1.3}$	$0.41^{<0.1}$	$15.29^{2.1}$	$92.92^{14.4}$	8.7×10^{-3}	42.17	2.16	4.71
				Dietary Strategy					
Carnivore	$16.12^{1.1}$	$35.5^{0.8}$	$0.32^{<0.1}$	$16.24^{2.8}$	$93.51^{17.8}$	8.6×10^{-3}	40.85	4.86	6.06
Herbivore	$13.25^{1.7}$	$32.88^{1.8}$	$0.45^{<0.1}$	$12.08^{2.1}$	$94.43^{12.6}$	7.6×10^{-3}	46.48	-4.93	5.43
				Body Size					
< 2.5mm	$15.41^{1.2}$	$34.11^{1.7}$	$0.42^{<0.1}$	$15.14^{2.2}$	$87.42^{15.7}$	8.6×10^{-3}	42.06	0.82	5.07
> 2.5mm	$13.62^{1.8}$	$34.28^{1.7}$	$0.41^{<0.1}$	$12.95^{2.6}$	$104.6^{15.1}$	7.8×10^{-3}	46.06	0.73	5.24

Table 1. The mean niche values (mean ^{SE}) of the 5 most important environmental parameters for each biological trait 1) Diapause behavior – Yes/No, 2) Dietary strategy – Carn (Carnivore), Herb (Herbivore) and 3) Body size – < 2.5mm and > 2.5mm for historical (1951-2000) data. Also shown are the mean biogeographical parameters for each trait group. Estimates of the total habitatarea (Area km^2) and the central position of the core range (Hist lat) are shown

for the historical period (1951 – 2000). The projected changes to the total habitat area expressed as a % of the historical area (Fut/Hist %), and the rate of species movement per decade (Movement, km dec^{-1}) between the future and historical period is also shown. For bearing see Figure 2b.

Figure 1: (a) The projected change in sea-surface temperature (SST - °C) between the future and historical period, (b) the Bray-Curtis similarity between the projected future and historical communities at each grid box, (c) the relationship between Bray-Curtis similarity and the corresponding difference in the projected future and historical annual mean ocean temperature, and (d) the projected change in the species richness of the copepod communities between the future and historical period. Warmer colours indicate areas with the largest increases in SST (a), areas with the highest Bray-Curtis similarity (b) and the largest increases in species richness (d). A vertical dashed line on panel (c) corresponds to locations with no mean temperature change between the historical and future periods. Dashed lines on panel (d) indicate the 50% contour for species richness change. Projected changes in additional environmental conditions are shown in S Fig 1.

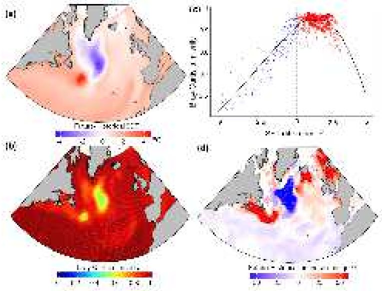
Figure 2: (a) The change in the central position of the biogeographical range of each species between the present (1951-2000) and future (2051-2100) periods. The arrow origin is the position in the historic period and the end the position in the future period. (b) The same changes, but with all vectors starting at the same location to highlight the relative distance (km) and direction of the change in the central position of each species' biogeographical range between the historical and future periods. The direction of movement are coloured based on the net northward (red lines) or net southward (blue lines) movement of each species to aid visualization.

Figure 3. The changes in the central latitude position (CL, °) and the percentage change in total habitat area (HA) are calculated for each herbivorous (n = 21 - green triangle) and carnivorous (n = 22 – red circle) species. Linear regressions are: $HA = 13.48*CL + 2.1$ ($R^2 = 0.38$) for carnivores (solid black line) and $HA = -10.3*CL+0.75$ ($R^2 = 0.49$) for herbivores (dashed black line). The dashed grey lines show the zero x and y intercept.

Figure 4: The mean time of peak prevalence in decimal months (e.g., June 15th = 6.5 as June is the 6 month and 15/30 = 0.5) for each species in the copepod community is averaged to quantify the peak of the copepod community throughout the North Atlantic. The panels show the timing of peak prevalence during the (a) historical (1951-2000) and (b) future periods (2051-2100) and the (c) difference in mean timing between the two periods. Warmer (cooler)

colors in panel (c) correspond to regions where the peak prevalence occurs later (earlier) in the year in the future period.

Figure 5: The percentage change at each 1 x 1° cell (left column) and the latitudinal average (mean ± 95% CI) in percent change (right column) for: (a, b) Diapausers, (c, d) Carnivores, and (e, f) Large copepods (>2.5mm) between the future and historical period. Negative percentage values (blue on the maps) indicate areas that show an increase in the number of non-diapausers (a, b), herbivores (c, d) and smaller sized species (e, f) in the future period.



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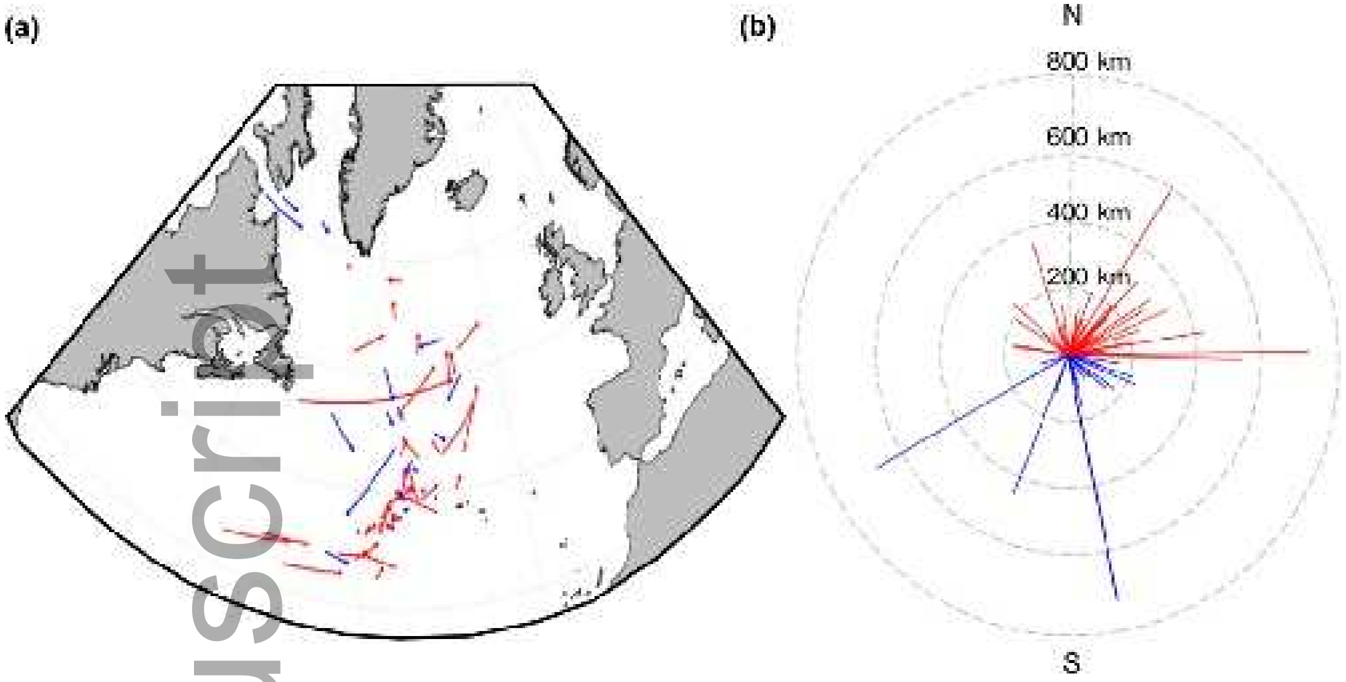

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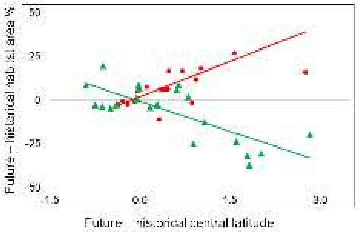

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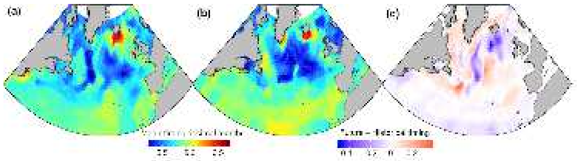

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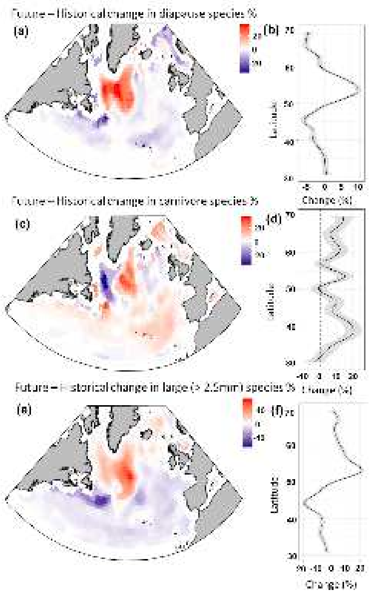

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