

Traits structure copepod niches in the North Atlantic and Southern Ocean

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ABSTRACT: Realised niches describe the environmental and biotic conditions that a species occupies. Among marine zooplankton, species traits, including body size, dietary mode (herbivore, omnivore, or carnivore), and diapause strategy are expected to influence the realised niche of a species. To date, realised niches are known for only a small number of copepod species. Here we quantify the realised niches of 88 copepod species measured by the Continuous Plankton Recorder (CPR) in the North Atlantic and Southern Ocean using Maximum Entropy (MaxEnt) modelling. We estimate the univariate mean niche, niche breadth of copepods for several important environmental variables, and assess the relative effects of several key zooplankton traits on the mean niche. Sea surface temperature (SST) contributed the most information to the description of niches on average across all species, with the rank importance of the remaining variables varying between regions. In the North Atlantic SST, depth, salinity and chlorophyll niches separated omnivores and herbivores from carnivores while in the Southern Ocean niche differences across dietary modes were found for chlorophyll and wind stress only. Diapausing copepods were found to occur in colder temperatures compared with non-diapausing taxa, likely because of their capacity for accumulating lipids. A strong negative body size–niche breadth relationship was found only for diapausing copepods, suggesting that larger multi-year generation species are more reliant on a specific temperature range to successfully reach diapause. Our analysis demonstrates strong connections between copepod traits and their realised niches in natural populations.

KEY WORDS: Copepods · Niche · Diet · Body size · Diapause · MaxEnt · North Atlantic · Southern Ocean

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INTRODUCTION

Marine zooplankton communities are diverse and transfer energy and organic biomass from primary producers to higher trophic levels (Hairston & Hairston 1993, Dickman et al. 2008). Copepods represent the most dominant fraction of zooplankton biomass in the temperate and polar water ecosystems (Verity & Smetacek 1996, Kjørboe 2011a) and are key contributors to carbon export via vertical migration and sinking pellets (Stamieszkin et al. 2015). Changes in copepod abundance (Beaugrand et al 2003, Chiba et

al. 2006) and distribution (Beaugrand et al. 2002) have occurred over decadal scales and have been shown to influence fish recruitment and changes in biodiversity (Pershing et al. 2005, Record et al. 2010, 2013). Anthropogenic climate change, through changes in temperature, salinity, light, nutrients, and other variables (Barton et al. 2016), has the potential to alter pelagic ecosystem communities. Understanding the temporal dynamics and spatial variations in zooplankton communities is a key challenge for ecologists. One approach to understanding the mechanisms causing these patterns is to classify organisms

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based on traits that affect fitness (McGill et al. 2006). For copepods, trade-offs in body size, dietary type, feeding and mating behaviours as well as dispersal capabilities all play roles in determining a species niche and their potential response to future climate-mediated changes in the ocean (Litchman et al. 2013).

Realised niches, which can be inferred from observations in natural communities, describe the environmental and ecological conditions in which individual species are found accounting for pressures in their habitat. The realised niche is often seen as a subset of the fundamental niche, which represents the range of optimal environmental conditions the species could inhabit in the absence of external pressures such as competition and predation. Detailed knowledge of realised niches for copepods will be valuable for understanding both their biogeographic distribution in the contemporary ocean and possibly for forecasting likely consequences of climate change. Based on broad scale differences in the realised niches among classes of phytoplankton in the North Atlantic (Irwin et al. 2012) and open ocean (Brun et al. 2015), we anticipate substantial structure in the copepod niches across species. For copepods, we expect that species traits (i.e. species characteristics that determine its fitness in a given environment; see Litchman & Klausmeier 2008) might be useful in understanding the variations in niche mean and breadth for a range of important environmental drivers and key species.

Body size is one of the most important traits for both phytoplankton and zooplankton (Barton et al. 2013a) and acts as a master trait due to its influence on the other traits (Kjørboe & Hirst 2014). Copepods have body sizes ranging from ~0.4 mm to over 1 cm in length. Body size is known to have an effect on the feeding (Kjørboe 2011b) and growth rates of an individual. Changes in ocean temperatures have an effect on body size, with higher temperatures resulting in smaller body sizes within species (Record et al. 2012) and at the community level (Beaugrand et al. 2003). As a result, copepods in higher latitudes generally have larger body size (San Martin et al. 2006). We hypothesise that variations in niche mean and breadth across species can be explained, in part, by variations in body size. It is possible that competitive interactions and other factors structuring communities will affect the relationship between traits and a species niche (Horne et al. 2016).

While almost all copepods engage in a certain level of omnivory and may alter their dietary strategy under changing local conditions (Turner 1984, Kleppel 1993), the majority of species are found to prefer one dietary type over another. They can be classed as an

herbivorous (e.g. eating phytoplankton) grazer or a carnivore (e.g. eating ciliates up to smaller zooplankton) (Turner 1984, Mauchline 1998, Richardson & Schoeman 2004). Because of their obligate requirement for primary producers as prey, we anticipate that chlorophyll biomass will be an informative variable for characterising the niches of herbivorous copepods. The principal feeding modes employed by copepods are filter, cruise and active ambush feeding and the selection of each feeding mode is dependent on metabolic trade-offs (Kjørboe 2011b). Several species can readily switch between feeding modes according to the prey availability in the area (e.g. *Acartia tonsa*, Jonsson & Tiselius 1990). Feeding mode is partially related to dietary strategy, in that filter current feeding is a feeding approach suited to capturing non-motile prey such as diatoms, while cruise or ambush feeding techniques require the individual to actively seek their more motile prey such as smaller zooplankton species and copepod nauplii (Kjørboe 2011b). Compared with dietary strategy, feeding mode is more strongly linked to the morphology of the individual and has been shown to affect prey selection and predator avoidance in addition to the simple act of capturing food (Kjørboe 2011b).

Several species of copepods undergo a period of dormancy in the winter months where their success is dependent upon acquiring sufficient lipid stores over the preceding productive season (Maps et al. 2014). The lipid reserves are required for the continuation of their life history cycle with several species utilising lipid stores for egg production when they emerge from diapause (Madsen et al. 2001). Ocean temperatures play a role in the development of diapausing species with many arctic species adopting multi-year lifecycles (e.g. *C. hyperboreus* and *C. glacialis*) due to the low temperatures which limit growth and development rates (Lynch et al. 1998, Falk-Petersen et al. 2009). These limitations may prevent the smaller temperate diapausing species such as *C. finmarchicus* from colonising arctic locations, as temperatures are simply too low for sufficient growth and development over the productive season (Ji et al. 2012). We therefore hypothesise that the temperature niches of diapausing and non-diapausing species are structured differently.

The spatial and temporal surveys conducted by the Continuous Plankton Recorder (CPR) survey in the North Atlantic and Southern Oceans provide a uniquely powerful dataset for investigating copepod niches. We use a species distribution model (SDM) to model the realised niches of the copepods sampled in these surveys. SDMs can be used to model the likeli-

hood of a species being found in a particular range of conditions by correlating the abundance or occurrence of each species with the environment in which it is found in (Elith & Leathwick 2009). We limit our study species to calanoid copepods (hereafter referred to simply as copepods) due to their widespread distribution and numerical abundance in the ocean (Kiørboe 2011b) and the availability of information related to their functional traits (Kiørboe 2011b, Litchman et al. 2013).

The North Atlantic and Southern Ocean CPR are the longest running large-scale spatial surveys, presenting an exceptional dataset for the analysis of copepod niches. We use these survey data together with climatological data on physical and chemical conditions to characterize the realised niches for the best sampled species. We assess the relative importance of each predictor variable in the determination of the realised niche and assess how realised niches differ across groups of species according to key traits including dietary strategy, body size, and the ability to diapause. We contrast realised niches across 2 areas with varying environmental conditions and trophic food web structures to test the robustness of our analysis. For several environmental variables the ranges of environmental conditions differ between the 2 regions (e.g. lower minimum temperatures, stronger wind stress, and narrower salinity ranges in the Southern Ocean). While copepods are pivotal in structuring trophic food webs in the North Atlantic (Hátún et al. 2009), Antarctic krill (*Euphausia superba*) is seen to be much more important to the Southern Ocean food web (Croxall et al. 1999, Murphy et al. 2007). Because previous studies have shown that niche models for one region may not apply to another, we develop separate niche models for the 2 regions (Torres et al. 2015). We anticipate that niches and their relationships to traits may contrast across ocean regions due to the varying ranges in environmental conditions and a difference in the plankton community structure, emphasising the importance of understanding relationships between species traits and relative niches when applying niches to climate change projections.

METHODS

CPR data

We examine 2 ocean areas with contrasting environmental conditions: the northern North Atlantic between $\sim 40^\circ$ to 60° N and the Southern Ocean, with

a focus on the region between Australia and Antarctica bounded by the latitudinal coordinates 35° to 75° S (Fig. 1). The biological data are derived from samples collected by the CPR, which is a plankton sampler towed by ships of opportunity along regular shipping routes at a depth of ~ 7 m. Water continually passes through the sampler via a small aperture (1.27 cm^2) and plankton are caught on silk gauze that moves such that each gauze panel represents 3.1 m^3 of water sampled for every 18.5 km of distance travelled (Warner & Hays 1994, Richardson et al. 2006). Zooplankton and phytoplankton have been sampled with consistent methodology since 1931 and 1958, respectively. The survey has covered much of the North Atlantic with $\sim 250\,000$ samples collected since 1958, and a number of sister surveys continue to be established in other oceans.

The Scientific Committee on Antarctic Research (SCAR) Southern Ocean Continuous Plankton Recorder Survey (SO-CPR) has been the major zooplankton monitoring programme for the Southern Oceans since its initiation in 1991. It now includes large consortia of countries that are involved with data acquisition (McLeod et al. 2010). The SO-CPR

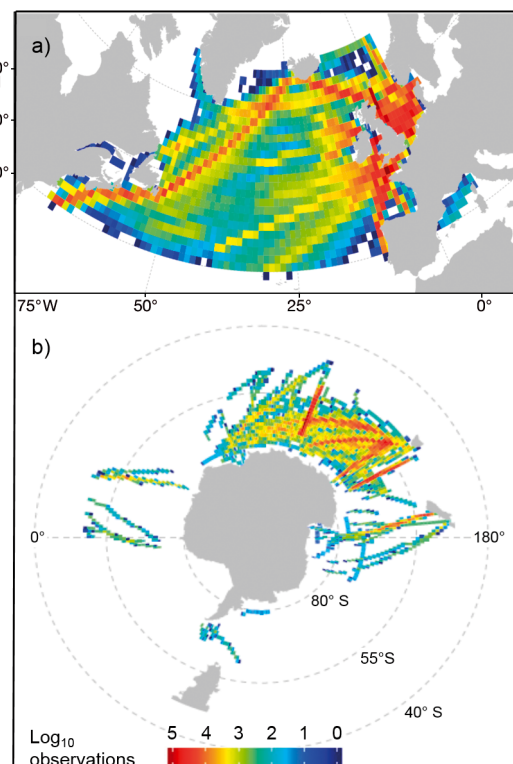


Fig. 1. Frequency and location of the CPR data in the (a) North Atlantic and (b) Southern Ocean. Warmer colours (from left to right) represent a higher frequency of CPR observations in a $1^\circ \times 1^\circ$ grid cell. Frequencies are reported on a log_{10} scale

survey has focused on enumerating zooplankton only, which has allowed for greater detail in the taxonomic identification of zooplankton species (sorting by sex, greater taxonomic resolution for taxa commonly overlooked in the North Atlantic). However, across both datasets copepods are still the most numerous in terms of abundance and number of taxa in each dataset. Almost 92% of the copepod taxa have been identified to species level (Richardson et al. 2006), while the remaining species are identified to genus level. While smaller copepod taxa such as *Oithona* and *Oncaea* spp. can comprise a significant fraction of the overall zooplankton biomass (Gallienne & Robins 2001), we omitted these species as the CPR does not resolve these groups to species level.

Copepod traits

For each taxon, functional trait values describing the dietary preference, feeding mode, diapause and body size were compiled from several published databases. Dietary preference was divided into 3 categories: herbivore, omnivore and carnivore. Copepods are seen largely as obligate omnivores but there exists a large degree of variation between species with a preference shown for carnivorous or herbivorous diets in the extreme ranges. Mandible morphology, for example, might be better suited to puncturing motile prey or for crushing diatoms (Michels & Schnack-Schiel 2005). Diets appear to be more influenced by food availability (Stevens et al. 2004) and concentration (Saiz & Calbet 2011), with diatoms being preferred when concentrations are high. Recent studies using stable isotope and fatty acid markers to assess dietary preference have shown that even with seasonal changes in variability, the trophic position (i.e. the long term dietary strategies) does not change significantly (El-Sabaawi et al. 2009). For the majority of the taxa found in both the North Atlantic and Southern Ocean database, information on their dietary type was obtained from Richardson & Schoeman (2004) and from the Mediterranean copepod trait database (Benedetti et al. 2016). Feeding mode relates to the behaviours adopted by copepods when capturing prey (Kiørboe 2011b). These data were obtained from the trait database compiled by Brun et al. (2017). Species were either classed as filter current feeding (creating feeding currents to capture prey), cruise feeding (actively swimming to capture prey) and mixed feeding for species known to engage in more than one feeding mode. Ambush feed-

ing (waiting for approaching prey) is found to mostly occur with cyclopoid copepods (e.g. *Oithona* spp.) and while sometimes used by copepods in this study it is not a common feeding mode. Therefore, we do not consider ambush feeding in this study. The body size for each taxon was obtained from Copépodes planctoniques marins (Razouls et al. 2018). We used the mean total length of an adult female (from rostrum to furca) as relatively few captured copepods are male (Mauchline 1998). A period of dormancy can occur at almost any stage of the life cycle for copepods, including diapausing or resting eggs (Mauchline 1998). For juvenile and adult stages, diapause is identified as a period of reduced metabolic activity, an increase of lipid stores and is usually associated with a change in vertical distribution (Conover 1988, Hirche 1998, Ohman et al. 1998, Maps et al. 2014). Species such as *C. finmarchicus* undergo the traditional pattern of diapause dormancy with a synchronous descent of the CV stages into deeper waters over winter across much of its distribution (Johnson et al. 2008). For others, a biphasic life history is found, where some individuals remain active in the upper layers with a deep-water component of multiple stages in deeper waters (Ohman et al. 1998). While some species in this list have definitive diapausing behaviour, there are others where evidence suggests diapause behaviour with only a subset of the characteristics present (e.g. arrested reproductive development and reduced metabolic activity, but no deep-water migration). For example, the copepod *C. helgolandicus* exhibits a shorter ~2 mo period of active dormancy compared to its congeners (Wilson et al. 2015), with reduced respiration rates but no deep-water migration (Bonnet et al. 2005). Several species not traditionally seen as diapausing species appear to do so regionally, such as *Metridia lucens pacifica* in the Japan Sea (Hirakawa & Imamura 1993) and *Calanus propinquus* in the Weddell Sea (Bathmann et al. 1993). We initially selected all species classed as diapausing species within the trait database compiled by Brun et al. (2017). We explored the available literature for these species and retained those with direct observations of diapausing behaviour (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m601p109_supp.pdf). This does not serve as an exhaustive search but allows us to select potential diapausing species without any bias caused by an ad hoc selection of diapausing and non-diapausing species. Details on the taxa used, their prevalence within our sampling areas, and all their functional traits can be found in Table S2 in the Supplement.

Biotic and abiotic variable selection

Variables that may influence the niche either directly (e.g. by altering metabolic processes or growth rate) and indirectly (e.g. the hydrodynamic forces that influence an individual's movement and transport) were selected based on evidence known from the literature. The environmental data were obtained from various sources including *in situ* measurements from ships and data buoys to create regular 1° grids of monthly (1950–2014) (Hadley SST2, Rayner et al. 2006) or climatological grids (World Ocean Atlas; Boyer et al. 2013). Data were also derived from satellite data (e.g. chl *a*; GlobColour, <http://glob.colour.info>) which were aggregated into climatological 1° grids from their grid size of 9 km² (Table 1). The CPR samples were aggregated into the same 1° grids as the environmental data with species indicated as present if found at least once in a grid square during a particular month. Only SSTs were directly linked to the CPR by matching samples collected at the same time and within the same 1° grid. For the climatological variables the environmental data were linked by matching samples collected within the same month and within the same 1° grid.

SST is known to influence species at an individual level by affecting physiological processes, which manifests itself at the population level by altering the distribution, abundance, and timing of the species (Speirs et al. 2006, Record et al. 2010). Similarly, salinity and oxygen levels could also affect the physiological processes of an individual depending on their tolerances of saline or hypoxic and anoxic environments. Mixed Layer Depth (MLD) is an indicator of water column stability and has been shown to influence the spatial distribution of *Calanus finmarchicus* in the North Atlantic (Reygondeau & Beaugrand 2011). Bathymetric depth has been suggested to be an important parameter that influences copepod bio-

geography (Beaugrand et al. 2003) and has been used as a variable to model the niche of *C. finmarchicus* (Helaouët & Beaugrand 2007). GEBCO is a global topographic dataset with (1') spatial resolution (www.ngdc.noaa.gov/mgg/gebco/; IOC, IHO, and BODC 2003). We chose to square-root transform the bathymetry data to aid visualisation of the niches. This did not influence the results of the modelling when compared with using actual values. Eddy kinetic energy (EKE, cm² m⁻²) is used as a proxy for eddy-mediated dispersal, but is also linked to prey availability and environmental conditions. Sea surface winds play an important role in mixing the ocean surface and setting temperature and nutrient regimes, and introduce turbulence which has been found to affect predator–prey encounter rates (Rothschild & Osborn 1988) and perhaps plankton community structure (Barton et al. 2013b). Both EKE and wind stress were obtained from the Aviso dataset (see the Aviso website; <https://www.aviso.altimetry.fr>). Finally, we also examine how chl *a*, as a proxy for phytoplankton biomass and hence food availability, influences the distribution of zooplankton (Frost 1972, Beaugrand et al. 2013).

MaxEnt modelling

The maximum entropy modelling framework (MaxEnt, Phillips et al. 2004, 2006) estimates the probability of presence of each taxon along each environmental variable as well as the probability of presence at each geographic location using the suite of environmental variables used in the model. MaxEnt estimates the probability of a species occurrence by comparing the environmental conditions where a taxon is present with all possible combinations of available environmental conditions. The resulting output is a response function

Table 1. The 8 biological and environmental variables used in the analysis, the data source, spatial and temporal resolution of the raw data if applicable and the type of data used (climatology or actual data matchup between CPR taxon occurrence and environmental variables)

Variable (unit)	Source	Input resolution	Type
Sea surface temperature (°C)	Hadley SST	Monthly 1°	Month / Year
Bathymetric depth (m)	GEBCO	NA 0.16°	NA
Salinity (PSU)	World Ocean Atlas 2015	Monthly 1°	Climatology
Chl <i>a</i> log ₁₀ (mg m ⁻³)	GlobColour	Monthly 9 km ²	Climatology
Eddy kinetic energy (cm ² s ⁻²)	Aviso	Monthly 0.25°	Climatology
Mixed layer depth (m)	World Ocean Atlas 2015	Monthly 1°	Climatology
Wind stress (N m ⁻²)	Aviso	Monthly 0.25°	Climatology
Oxygen saturation (%)	World Ocean Atlas 2015	Monthly 1°	Climatology

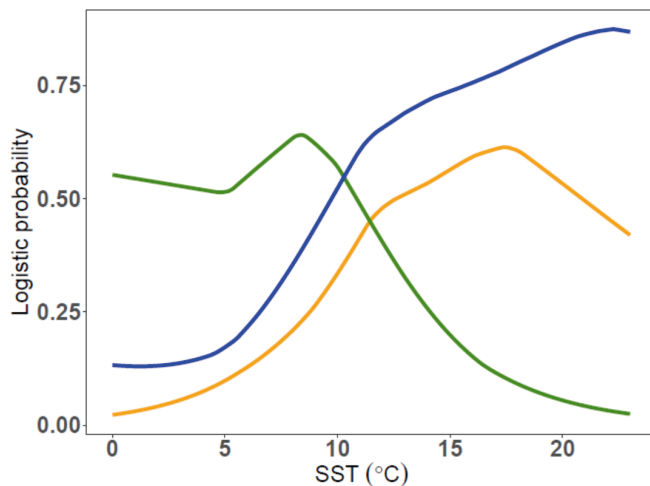


Fig. 2. Three univariate response curves showing the logistic probability of occurrence as a function of SST for an herbivore (*Calanus finmarchicus*: green), omnivore (*Pleuromamma gracilis*: blue), and carnivore (*Candacia armata*: orange) species in the North Atlantic

which shows the logistic probability of a species presence for all environmental conditions. Fig. 2 shows the response functions of 3 species to SST in the North Atlantic. Of the many potential SDMs available, MaxEnt has consistently been shown to be one of the best regarding the accuracy of its estimated probabilities (Elith et al. 2006, Duan et al. 2014).

Our model selection procedure followed the same methodology used in Irwin et al. (2012). Initially, data were randomly separated into a training and testing dataset in a 3:1 ratio. For each taxon, the MaxEnt model was run on the training dataset using 100 bootstrap resampling runs. To keep the modelling consistent for each taxon, all changeable parameters within the MaxEnt program were maintained at their default settings with the exception of allowing for threshold response functions, which were disabled. Threshold responses can produce step-wise changes in the response curves which are often difficult to interpret and will increase the chances of overfitting the data (Elith et al. 2011). The testing dataset is then used as an independent sample to test the accuracy of the model by predicting the training model on the testing data and evaluating its performance at correctly predicting the species presence. The receiver operating characteristic (ROC) curve plots the rate of correct presence assignments (true positive) versus the incorrect presence assignments (false positive) that the model produces from the testing data. The area under the

curve (AUC) is calculated for each ROC curve where values approaching 1 suggest a higher probability that a model will correctly assign a species presence to a location while values closer to 0.5 suggest that this model will correctly assign a species presence no better than chance. Solely relying on the AUC for evaluating model performance has been shown to be problematic in certain cases, particularly when evaluating species with a small number of observations (Lobo et al. 2008, Yackulic et al. 2013). We followed similar protocols outlined by Barton et al. (2016): requiring a minimum of 30 observations of each taxon analyzed (Hernandez et al. 2006) to reduce sampling bias errors due to restricted or noisy distributions and raising the minimum AUC for inclusion to 0.6 therefore removing those species where the models had shown to be poor predictors of species presence. We retained a total of 88 copepod taxa with 64 remaining in the North Atlantic and 24 in the Southern Ocean. Of the 88 taxa, 80 had an AUC >0.8 for the full model using testing data (0.86 ± 0.08). The remaining taxa were the most abundant in our dataset and often exhibited a cosmopolitan distribution, a result also observed for phytoplankton in the North Atlantic (Barton et al. 2016). This is a known limitation of the MaxEnt procedure when the measured species is found across a large proportion of the available variables' ranges (Elith & Leathwick 2009). Despite this, the remaining taxa had an AUC >0.65 for the full model using testing data.

We focused on the response functions for each environmental variable as those generated by the full model are partial response functions with an averaging across the other variables that often hides the effects of strongly correlated variables (Phillips et al. 2004, Buermann et al. 2008). The permutation importance gives the percentage importance of each environmental variable in estimating the probability of occurrence for each species. Models are run with each environmental variable sequentially removed and the resulting change in AUC is measured. Larger decreases in AUC signify a high variable importance, and the changes in AUC values are normalised to give the resulting percentages.

Statistical analysis

We estimated both the probability of presence of each taxon along each environmental variable as well as the probability of presence at each geographic location using the suite of environmental

variables used in the model. Here we focused on the univariate response functions, calculating the niche for each taxon in terms of only one variable at a time. We used the response functions to find the mean niche and the niche breadth by calculating the weighted mean (μ) and weighted standard deviation (σ) of each environmental variable, using the logistic probability response curve as the weight function. All species have a unimodal logistic probability response curve with a clearly resolved peak allowing us to interpret the weighted mean as the mean niche for each variable. The realised niche can be broken down into 2 components where the mean niche provides information on where along an environmental gradient a species is most likely to be found while the standard deviation can be interpreted as a niche breadth showing the ranges of each species along each variable gradient. The 100 bootstrap reruns provide an estimate of 95% confidence intervals of the mean niche and niche breadth for each taxon.

A Tukey's honestly significant difference (HSD) test was used to evaluate differences in the mean niche of species grouped according to their dietary strategies and feeding modes along each univariate variable gradient. Owing to the differences in the background data for many of the univariate variables in both areas (different ranges in environmental data) only within-basin comparisons between traits are performed.

The relationship between the mean taxon body length and mean niche was explored by performing a regression for each of the 8 environmental variables. We combine the 88 taxa into the same model for this analysis, as we are interested in exploring the scalar response of size to the mean niche of an environmental, or in the case of chl *a*, a biological, gradient. Even with different ranges of background data between the 2 areas, we expect that the relationship would continue along that gradient (i.e. mean species size changes in a consistent direction with an increasing variable value even when no overlapping data are available). Finally, we analysed taxa according to whether they had a known diapause strategy and those where diapause had not been observed. A total of 18 out of 88 copepod species were found to undergo diapause during one or more of the copepodite stages. We examined the difference in the mean niche of diapause and non-diapause taxa along the temperature gradient using ANOVA and examined the relationship between niche breadth and body size (which serves as a proxy for growth rates and generation time) of diapause and non-diapause species.

RESULTS

For taxa with at least 30 observations throughout the whole grid, a total of 320 055 observations were found across the 64 taxa in the North Atlantic while for the Southern Ocean a total of 18 104 observations were found for the remaining 24 taxa. There were 5 taxa found to be common in both the North Atlantic and Southern Ocean, and these were treated as separate populations within each ocean basin (see Table S1 in the Supplement). The AUC scores range from 0.68 to 0.90 for the multivariate MaxEnt models indicating that the models have a strong likelihood of correctly predicting a species presence along each environmental gradient. AUC scores vary little (about 0.02 on average) between the training and testing datasets suggesting strong predictive capabilities with our models (see Table S1). The most informative predictors based on the AUC are SST, salinity, depth, and wind stress. In the North Atlantic the 4 most important variables are shared among the 3 dietary strategy groups with chl *a*, bathymetric depth (depth), SST, and eddy kinetic energy (EKE). These variables were the greatest contributors to the overall permutation importance for carnivores (75.3%), omnivores (72.9%), and herbivores (75.7%) (Fig. 3). The importance of these 4 variables differs between dietary strategies with SST being the most important for carnivores, depth for omnivores, and chl *a* for herbivores. In the Southern Ocean however, the most important variables differ across dietary strategies. Only SST appears as 1 of the 4 most dominant variables for each dietary strategy (Fig. 3). For carnivores, SST, wind stress, mixed layer depth (MLD), and oxygen saturation (oxygen) comprise 69.4% of the total importance. For omnivores, SST and salinity contribute almost the same level of variable importance (68.7%) as the 4 most important variables for carnivores (Fig. 2). SST comprises almost 45% of the total permutation importance for herbivores followed by oxygen (17.1%) and MLD (11.6%) contributing a total of 73.7% to the total importance (Fig. 3).

Body size and environment

Out of the 8 variables examined, 3 were found to have a significant relationship between the mean body size and the mean niche: chl *a*, wind stress, and SST (Fig. 4, $p < 0.05$). The amount of variance in mean niche explained by mean size was low with R^2 values of 10, 17, and 14% for chl *a*, wind stress, and SST, respectively. These significant negative rela-

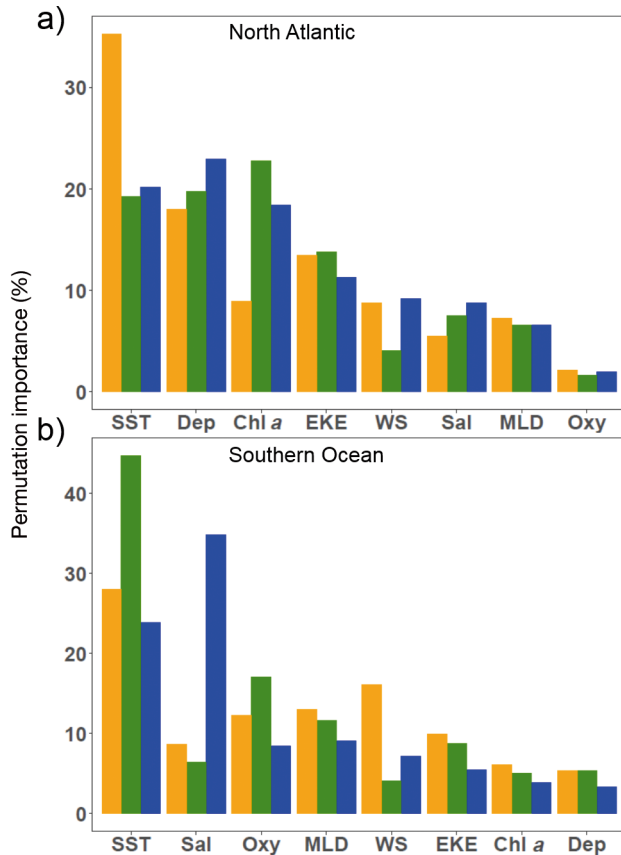


Fig. 3. The permutation importance quantifies the contribution of each variable to the final model output. The mean importance for each of the 8 variables in the (a) North Atlantic and (b) Southern Ocean is ordered from the most important to least important. The colours identify each dietary strategy: carnivores (orange), herbivores (green), and omnivores (blue)

tionships also exist within each region. The strongest relationships are found within the Southern Ocean with R^2 values of 13, 25, and 26% while in the North Atlantic these R^2 values are 10, 13, and 14% for chl *a*, wind stress, and SST, respectively. The negative relationships between mean size, chl *a*, and wind stress are somewhat surprising, a pattern we will revisit in the 'Discussion'.

Univariate niches and differences in dietary strategy

We found that dietary strategy showed the most differences between the trait categories (herbivore, omnivore, and carnivore) while feeding mode (ambush, cruise, and filter) was unsuccessful at distinguishing differences in the mean niche along each environmental gradient. SST represents one of the

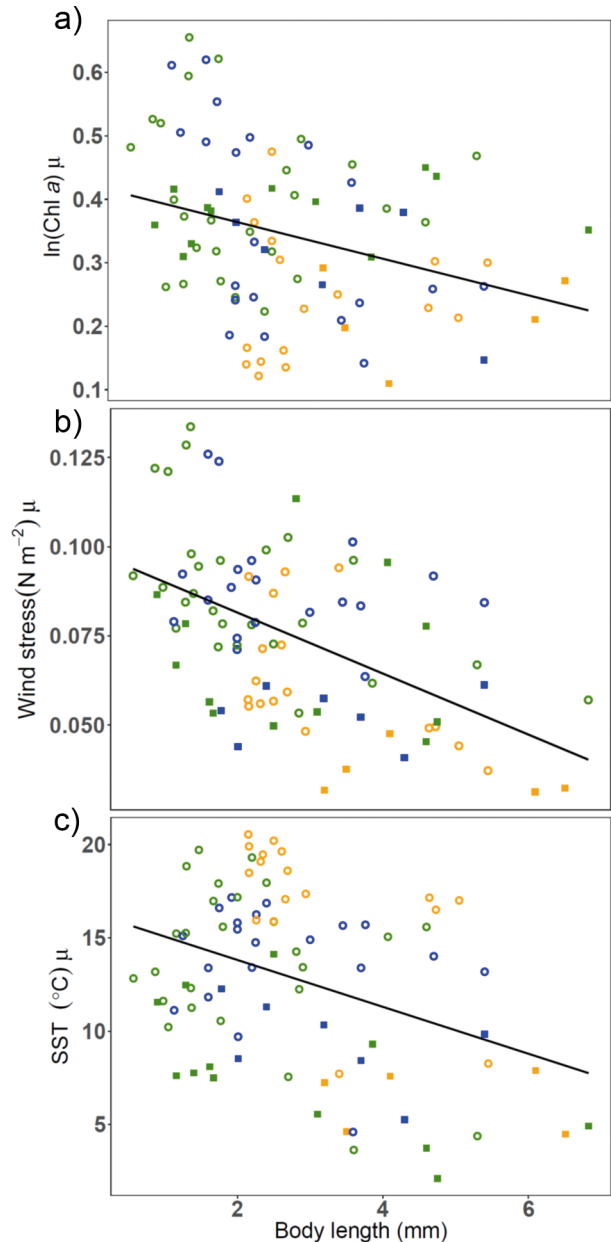


Fig. 4. Mean niche (μ) and the mean body length for each of the 88 taxa in the North Atlantic (solid symbol) and Southern Ocean (open symbol). Shown here are the 3 variables that were found to have a significant relationship between the mean niche and mean size: (a) chl *a*, (b) wind stress, and (c) SST. Coefficients of determination and p-values for *t*-test on slopes: $R^2 = 0.10$, $p = 0.002$; $R^2 = 0.17$, $p < 0.001$; $R^2 = 0.14$, $p < 0.001$ for chl *a*, wind stress and SST, respectively

most important variables for all taxa in both basins and is one of the 3 most important variables for each dietary strategy (Table 2). The Southern Ocean has a much colder regime than North Atlantic with a mean temperature of 5°C compared with 11°C in the North Atlantic. As a result we see that the mean niches of

Table 2. AUC score of each variable and the full (testing) model for the 3 dietary strategies (carnivores, omnivores and herbivores) in the North Atlantic and Southern Ocean. Number of species analyzed for each feeding strategy and ocean basin is reported as n

Variable	North Atlantic			Southern Ocean			Overall
	Carnivore (n = 17)	Omnivore (n = 19)	Herbivore (n = 25)	Carnivore (n = 5)	Omnivore (n = 6)	Herbivore (n = 13)	
SST	0.78	0.70	0.68	0.69	0.78	0.70	0.74
Salinity	0.78	0.77	0.72	0.63	0.75	0.67	0.74
Wind stress	0.72	0.69	0.71	0.65	0.74	0.72	0.72
Depth	0.75	0.75	0.70	0.65	0.65	0.63	0.69
Chl a	0.69	0.70	0.65	0.62	0.62	0.63	0.64
MLD	0.65	0.63	0.59	0.65	0.61	0.68	0.63
Oxygen	0.64	0.64	0.64	0.66	0.62	0.63	0.63
EKE	0.65	0.63	0.65	0.62	0.66	0.64	0.62
Full model	0.89	0.86	0.83	0.82	0.86	0.84	0.82

species in the North Atlantic occur in significantly higher temperatures compared with the Southern Ocean (Fig. 5a). There is a sigmoid relationship between the mean niche and niche breadth in both areas with maximum niche breadths occurring at intermediate temperatures in both areas. There were no significant differences in mean temperature niches found across the dietary strategies in the Southern Ocean (Table 3). Significant differences were found between the mean temperature niche of herbivores and omnivores compared with carnivores in the North Atlantic (Table 3). In the North Atlantic, carnivores were found to occur on average in surface temperatures that were 2.9°C warmer than omnivores and 3.67°C warmer than herbivores. Herbivores were also found to have significantly broader niche breadths than carnivores by ~0.8°C.

Southern Ocean taxa were found in significantly deeper waters with larger niche breadths compared with the majority of the North Atlantic taxa (Fig. 5b). The histograms of the background data show that the Southern Ocean region is largely oceanic with bathymetry >1000 m while in the North Atlantic there are many shallower continental shelf areas present in the data. In the North Atlantic the bathymetric depth niches for omnivores and carnivores were found to be significantly different than the niches for herbivores, occupying shallower depths, although omnivores were found to have significantly narrower niche breadths than herbivores. In the Southern Ocean no significant differences were found between the niches of the 3 dietary strategies.

Chl a is one of the most important variables determining a taxon's niche in the North Atlantic and one of the least important in the Southern Ocean relative to the other univariate variables considered (Table 2). The mean chl a niche range in both ranges varies

between 0.12 and 1.85 mg m⁻³ with a steady linear increase in the niche breadth until ~0.4 mg m⁻³ (Fig. 5c). In both the North Atlantic and Southern Ocean, herbivores and omnivores were found to have significantly higher mean chl a niche than carnivores with a mean difference of 1.1 to 1.17 mg m⁻³ across the 4 pairwise comparisons (Table 3). For both the North Atlantic and Southern Ocean, herbivores were found to have significantly wider niche breadths than carnivores with a mean difference of 1.04 mg m⁻³ in both areas (results not shown).

Salinity varied more in the North Atlantic (from 32 to 37) than in the Southern Ocean (33.8 to 35) (Fig. 5d). Consistent with this difference in salinity variation, the salinity niche breadths of taxa in the Southern Ocean are much narrower than those in the North Atlantic. With the exception of omnivores in the Southern Ocean, the permutation importance for salinity is rather low in both seas, indicating that salinity variation is not usually a strong determinant of niches. Despite this, we find that there are significant differences in mean salinity niche among the dietary strategies in the North Atlantic with omnivores and herbivores found to occur on average in lower salinities compared with carnivores (Table 2).

Wind stress is of medium or low importance for all dietary strategies in both areas. We find that the mean niche and niche breadths are quite different in both areas despite similar ranges in environmental conditions (Fig. 5e). For increasing wind stress, there was an increase in niche breadth with increasing mean niche. Despite the narrower range of mean niches in the Southern Ocean, significant differences are found between the dietary strategies with herbivores and omnivores found to have higher mean niches for wind stress compared with carnivores (Table 3).

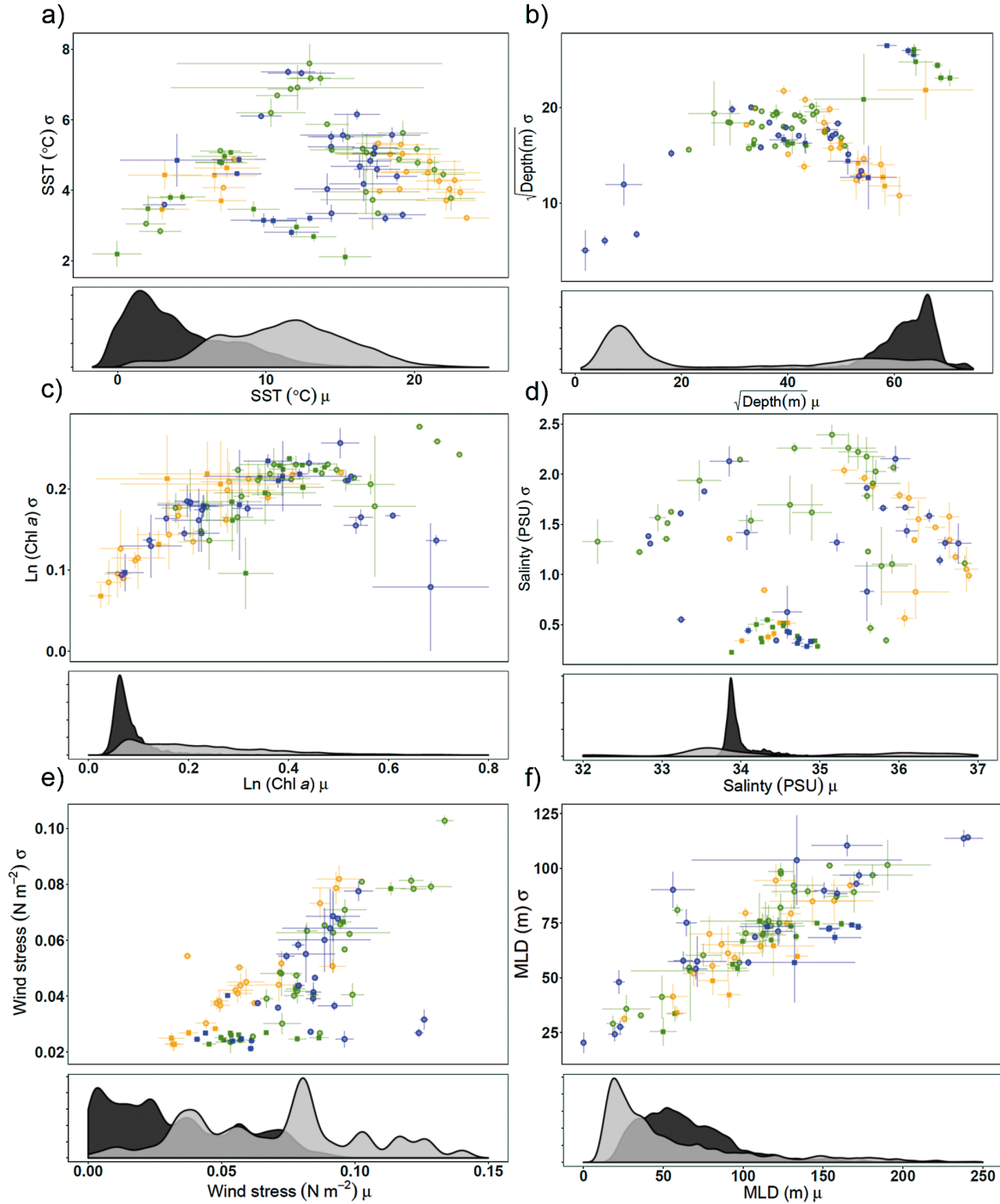


Fig. 5. The mean niche (μ) and niche breadth (σ) for each taxa in both the Southern Ocean (open symbol) and North Atlantic (filled symbol). The colours identify each dietary strategy: carnivores (orange), herbivores (green), and omnivores (blue). Each panel shows a particular univariate niche gradient with (a) SST; (b) $\sqrt{\text{Depth(m)}}$; (c) $\ln(\text{chl } a)$; (d) salinity (PSU); (e) wind stress; (f) MLD. The error bars represent the standard deviation of the mean niche and niche breadth from the 100 bootstrap simulations for each species. Beneath each panel is the frequency distribution of the background data from the Southern Ocean (black) and North Atlantic (grey)

Mixed layer depth (MLD) was of medium and low importance in both areas, however in the Southern Ocean omnivores were found in areas with significantly deeper MLD compared with herbivores and

carnivores (Table 3, Fig. 5f). The variables of kinetic energy and oxygen saturation were of low importance in both areas and were not shown to have any significant differences in the mean niche across the 3

Table 3. Pairwise differences of mean niches for each variable, averaged over species, across the 3 dietary strategies: carnivore, omnivore and herbivore for both the North Atlantic and Southern Ocean. Significant differences are in bold with significance levels denoted by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Variable	North Atlantic			Southern Ocean		
	Omnivore vs. carnivore	Omnivore vs. herbivore	Herbivore vs. carnivore	Omnivore vs. carnivore	Omnivore vs. herbivore	Herbivore vs. carnivore
SST	-2.9*	1.14	-3.67***	1.55	1.85	0.35
Depth	-9.8***	-2.3	-7.8**	-2.51	-2.61	-0.09
Salinity	-0.9**	0.21	-1.17***	0.15	0.18	0.03
Chl <i>a</i>	0.11**	-0.05	0.16***	0.10**	0.04	0.12**
Wind stress	0.001	0.001	0.001	0.003**	0.001	0.003**
MLD	4.9	0.9	3.8	44.5**	34.5*	10.3
Oxygen	0.14	-0.04	-0.07	0.59	0.83	0.24
EKE	0.01	0.01	0.01	0.003	0.004	0.001

dietary strategies. These data are not shown, but the results of the variable importance and niche comparisons can be found in Tables 2 & 3.

Diapause taxa were found on average to occur in waters that were $\sim 4.1^\circ\text{C}$ colder than non-diapause taxa ($F_{1,85} = 12.6$, $p < 0.001$, Fig. 6a). A strong negative relationship was found between the niche breadth and mean size of diapause copepods (Fig. 6b; $R^2 = 0.39$, niche breadth = $[2.22 \pm 0.61] + [-0.24 \pm 0.18]$ slope, $p < 0.001$) while the relationship for non-diapause copepods was non-significant (Fig. 6c; $R^2 = 0.03$, niche breadth = $[1.37 \pm 0.22] + [0.07 \pm 0.07]$ slope, $p = 0.09$).

DISCUSSION

Our analysis of the realised niches of 88 copepod taxa from Continuous Plankton Recorder (CPR) surveys in the North Atlantic and Southern Ocean has revealed several key features. Temperature, salinity, bathymetry, and chl *a* concentration are the most important determinants of the predictive skill of our niche models. The mean realised niche varies with traits including dietary strategy, body size, and diapause. These results are robust across 2 oceanic regions (North Atlantic, NA, and Southern Ocean, SO) with strongly contrasting environmental conditions.

The CPR data span large geographic and temporal ranges making them unparalleled observational data for plankton ecologists. No data are perfect, and the CPR surveys present many analytical challenges as well as opportunities. Particular concerns include sampling effort varying in space and time, sampling only in the surface ocean, the lack of simultaneous observation of environmental conditions, semi-quantitative observations of abundance, and variability in

detectability of individual taxa. The MaxEnt method mitigates some of these concerns by using only presence data (ignoring abundance) and assuming absence of observations of a species is not evidence of absence (this is the maximum entropy part of the model formulation). Pooling vast surveys across time (sampling time varies within a day, across seasons, and in multiple years) and space should lead to opportunities to observe species in the surface layer (7 m depth) even if they usually occur much deeper than this surface layer. Similarly, using climatological and environmental data results in a great deal of averaging, but the broad scale of sampling emphasises large-scale differences in environmental conditions and effectively ignores small-scale variability. Additionally, we note that the data are observational rather than arising from designed experiments, so our statistical analysis should be viewed primarily as generating hypotheses rather than testing hypotheses.

Which variables are most important for defining copepod niches?

Ocean temperature influences many aspects of a species' ecophysiology, including growth and feeding rates (Forster et al. 2011). This broad range of effects is reflected in the relative importance of SST in the determination of the realised niche. SST was the most important variable defining species' niches, on average, and was one of the most important variables for species across all 3 dietary strategies in both the North Atlantic and Southern Ocean (Table 2, Fig. 3). This dominant role of SST was anticipated based on previous studies that showed how changes in the seasonal timing of SST can alter the phenology of many plankton species (Edwards & Richardson 2004),

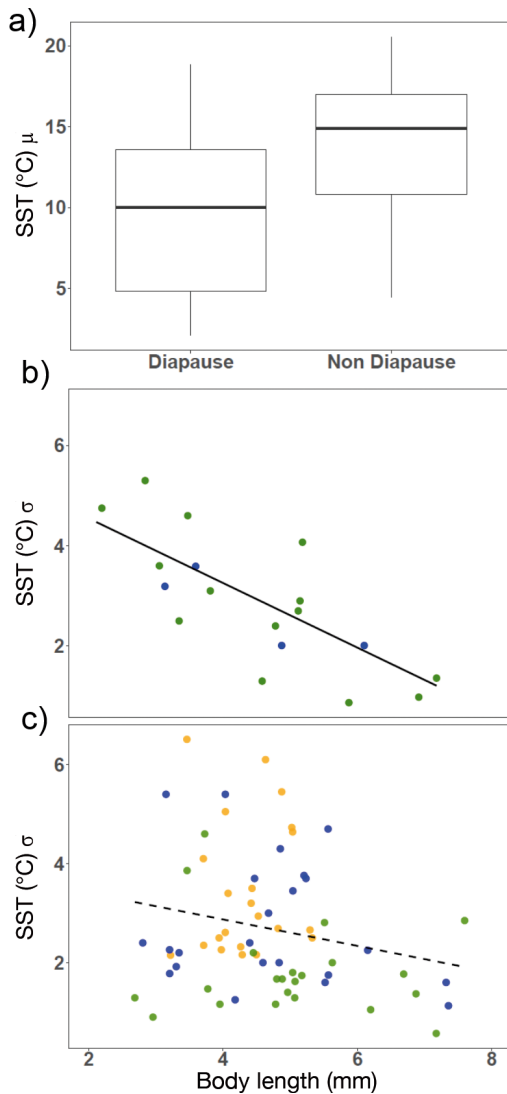


Fig. 6. The relationship between the SST niche and diapause and non-diapause taxa showing (a) a boxplot of the mean niche (μ) of diapause and non-diapause copepods. Boxes represent the median and quartile ranges. Whiskers delineate full ranges. Relationships between the mean body length and the SST niche breadth (σ) are shown for (b) diapause and (c) non-diapause copepods. The straight lines in (b) and (c) are regression lines with $R^2 = 0.39$, $p < 0.001$ for diapause and $R^2 = 0.03$, $p = 0.08$ for non-diapausing copepods. The solid line in (b) indicates a significant relationship, while the dashed line in (c) indicates an insignificant relationship between variables

causing timing mismatches and detrimental knock-on effects for higher trophic levels (Hipfner 2008, Burthe et al. 2012). Large-scale changes in the spatial distribution of plankton species may have been a result of environmental filtering of communities based on their niches as SST changes (Beaugrand et al. 2002). These observations and anticipated changes in temperature with climate change over the next

century underscore the importance of knowing temperature niches of individual taxa and how the temperature niches vary with key traits. The relative importance of SST was even more pronounced in the Southern Ocean compared to the North Atlantic despite the narrower range of SST variation in the Southern Ocean (Table 2, Fig. 5a). SST has not generally been found to be the most important driver of phytoplankton niches (Irwin et al. 2012, Barton et al. 2016), consistent with the observation that temperature has a stronger effect on the growth rate of heterotrophs and higher trophic levels compared to photoautotrophs (Edwards & Richardson 2004, Rose & Caron 2007). Our results reinforce previous analyses of temperature on copepods, supporting the importance of temperature for the realised niche and providing a quality check for our modelling efforts.

Following temperature, the next most important variables defining copepods' niches were salinity, wind stress, bathymetric depth, and chl *a* concentration although their relative importance differed across dietary strategies and the 2 oceanic regions. The single variable (Table 2) and the permutation (Fig. 3) importance did not always agree, so there is not a strong signal of the relative importance among these variables in the determination of the realised niche. Contrasting variable importance between regions and across dietary strategies reflect the importance of the range of available environmental conditions and traits in determining regions of occupied niche space. Salinity was an important factor structuring copepod niches (single variable models, Table 2) in both regions despite its relatively narrow range in the Southern Ocean, but provided relatively little additional information beyond the other variables (Fig. 3) except among the omnivores in the Southern Ocean. These results are consistent with the information contained in the salinity signal being largely related to correlation with other variables. The relatively high importance for omnivores in the Southern Ocean is surprising since the narrow range of salinity variation could be expected to be less informative than a broader range of variation; these omnivores may be especially sensitive to salinity changes. Wind stress is most important for carnivores in the Southern Ocean (Fig. 3) and broadly important as a single variable for all groups in both regions (Table 2), likely because of its effect defining the vertical structure and physical–chemical environment of the upper ocean. Bathymetric depth was a key variable in the North Atlantic, largely because it enables a distinction between copepods found primarily on the continental shelf and those found

in the open ocean. Chl *a* concentration was the most important variable for herbivores in the North Atlantic although its relative importance in the Southern Ocean was generally low. The mean chlorophyll niches are comparable between the 2 regions (Fig. 5c), but the environmental mean and variation in log chl *a* concentration is much less in the Southern Ocean, which may account for the difference in the importance of this variable in defining the niche.

How does dietary strategy affect the realised niche of copepods?

Differences in mean temperature, bathymetric depth, chl *a* concentration, and salinity realised niches of carnivores compared to herbivores and omnivores (Tables 2 & 3) appear to reflect physiological or ecological differences linked to the dietary trait. SST niches are higher in the North Atlantic compared to the Southern Ocean with a wider range of available temperatures allowing for a separation of copepod niches across feeding strategies (Table 3). Mean niches in the Southern Ocean for temperature, bathymetry, and salinity (Fig. 5a–d) are compressed into a smaller range compared with the North Atlantic, so that niche differences among the dietary groups detected in the North Atlantic for these variables may still exist, but can't be resolved in the Southern Ocean. These niche differences reflect the observation that warmer systems generally have complex trophic interactions with an abundance of carnivorous copepods leading to top-down dominated systems, compared to cooler seasonal systems that tend to be dominated by herbivorous copepods and which are dominated more by bottom-up processes (Hébert et al. 2017).

On average, we observe similar realised niches for omnivores and herbivores, possibly due to the selection of similar food resources by these groups during the spring and summer seasons. Relative levels of herbivory and carnivory are known to vary seasonally among omnivores from the family Metridinidae, which account for about 3-quarters of the omnivore sightings in this study. For example, diets of *M. gerlachi* (Calbet & Irigoien 1997) and *Pleuromamma xiphias* (Schnitzer & Steinberg 2002) show that up to 93% of the diets of these species can be phytoplankton during spring and summer before switching to a more varied winter diet. Herbivores and omnivores are generally found at higher chl *a* concentrations compared with carnivores in both oceans, consistent

with a significant advantage of high chl *a* concentrations for species directly feeding on phytoplankton. The role of dinoflagellates in copepod diets has been difficult to quantify (Kleppel 1993) and depends on several factors including dinoflagellate biomass and species type, but there is evidence that later blooming copepods (e.g. *Acartia* spp., *Temora* spp.) and estuarine species (*Eurytemora* spp.) show a preference for dinoflagellates (Rollwagen Bollens & Penry 2003). Indirect evidence from temperature and salinity niche relationships is consistent with feeding preferences of copepods. Larger diatom species typically dominate during the spring bloom period (Taylor et al. 1993, Barton et al. 2013b) and are associated with cooler temperatures and lower salinities in the North Atlantic reflecting the patterns observed for herbivorous copepods in this study (Irwin et al. 2012). We found that the herbivore species *Acartia danae* and *Temora stylifera* occur in higher SST compared with other herbivore and omnivore taxa suggesting that they occupy warmer waters or occur much later in the season to exploit the increase in dinoflagellate abundance (Irwin et al. 2012). We attempted to refine our chl *a* niche analysis by estimating the biomass of diatom and dinoflagellate groups approximately partitioning the chl *a* concentration across these groups using the CPR abundance data and the biovolume of each phytoplankton taxon. Unfortunately, this partition of chl *a* concentration into diatom and dinoflagellate sources was significantly less useful than simple chl *a* concentration in defining species niches for herbivores and omnivores.

The lower wind stress niche occupied by carnivores compared to herbivores and omnivores in the Southern Ocean may be a result of direct physical effects on the copepod and phytoplankton communities. Wind stress plays a strong role in the seasonal succession of phytoplankton with the non-motile phytoplankton (e.g. diatoms) often dominating during periods of higher wind stress often observed during the spring bloom period and persistent wind-driven mixing in the summer period maintains enhanced areas of chl *a*. Changes in wind stress are strongly correlated with turbulence in the upper ocean (MacKenzie & Leggett 1993), which in turn can influence the vertical positioning behaviour of copepods (Incze et al. 2001). Direct links between turbulence induced from wind stress and the finer scale turbulence that influences copepods directly such as altering feeding efficiency (Kjørboe & Saiz 1995) and grazer–prey encounter rates (Marrasé et al. 1990, Saiz & Kjørboe 1995) are very complex and difficult to explore at this scale.

How is body size related to the environmental niche?

Temperature, wind stress, and chl *a* concentration realised niches all vary with copepod body size across all feeding types and in both oceans (Fig. 4). The anticipated effects of climate change suggest that there will be a significant restructuring of the size-structure of copepod communities with consequences for trophic efficiency and carbon export or sequestration (Hébert et al. 2017). For example, regions of the ocean with higher temperatures, greater wind stress, and increased chl *a* concentrations in the future can be expected to have smaller copepods compared to the present (Fig. 4). Previous studies have shown that larger species dominate in northern, cooler waters and smaller species are more likely to be found in warmer, tropical waters in both the Atlantic (San Martin et al. 2006) and Pacific (Chiba et al. 2015) oceans. Increasing temperatures have been shown to result in decreases in the mean size and community structure in Long Island Sound and the Baltic Sea (Daufresne et al. 2009, Rice et al. 2015). As ocean temperatures increase over the next century, these changes are likely to shift communities into states where smaller phytoplankton and zooplankton species dominate, decreasing the fecal carbon flux (Finkel et al. 2010, Stamsieszkin et al. 2015, Brun et al. 2016).

Smaller copepods are found on average in locations with higher chl *a* concentrations and these smaller copepods are more likely to be herbivorous than omnivorous or carnivorous consistent with their prevalence at higher chl *a* concentrations. Since chl *a* concentration is generally higher at lower temperatures there may frequently be opposing effects on body size from temperature and chl *a* concentration. The community composition of phytoplankton, which can vary independently from chl *a* concentration, has been shown to significantly alter temperature–size responses in other areas (Diamond & Kingsolver 2010). The chl *a* concentration–body size relationship is partially attributable to the mean variation in body size of the different dietary strategists, since many of the largest taxa are carnivorous and do not prey on food containing chl *a*. Size-selective predation of copepods by planktivorous fish, a factor not included in this study, can result in a negative body size–productivity relationship (Bruce et al. 2010, Brun et al. 2016). Many of the variables influencing copepod presence are highly correlated, which creates complications for interpreting univariate niches, as illustrated here, but it is still possible to create robust

multivariate niches and predictive models for copepod biogeography (Table 2).

The increase in body size in lower wind stress environments may be linked to the dietary strategy of the copepods, although the interpretation of this signal is complicated by correlations between temperature and chlorophyll concentration. Herbivorous copepods tend to prefer the non-motile diatom cells (Mariani et al. 2013) which benefit from more turbulent environments compared with dinoflagellates that thrive in more stable stratified conditions. Diatoms are found under colder conditions with higher average chlorophyll concentrations compared to dinoflagellates (Irwin et al. 2012). As the herbivores are significantly smaller than the carnivorous copepods, we find that the smallest taxa would be found more often in higher wind stress areas.

What is the role of temperature in structuring the diapause life history strategy?

In high latitudes, copepods have adapted to large seasonal shifts in environmental conditions by adopting a diapausing strategy during the winter months. Our results demonstrated that diapausing taxa occurred most frequently in colder water with significant differences found between the mean niches of diapausing and non-diapausing groups. Diapause in copepods has been found to occur from the egg (i.e. resting egg) through to the naupliar and copepodite stages; however, we chose to focus only on those that have demonstrated diapause strategies in the copepodite stages (mainly CV), as these stages require the individual to acquire significant lipid reserves to meet overwintering demands (Ingvarsdóttir et al. 1999).

We found that for diapause taxa there is a significant negative relationship between the mean body size and niche breadth, while for non-diapause taxa no relationship was found (Fig. 6). We suggest that a reason for this relationship is increased phenological (i.e. life cycle timing) pressure placed on larger diapausing taxa that have generation times lasting a year or longer (e.g. 2 yr is commonly observed for *C. hyperboreus*, Ji et al. 2012). These taxa are presented with a narrower range of favourable temperatures that promote enough growth to achieve diapause restricting their overall niche breadth. By contrast, smaller diapausing taxa (e.g. *Pseudocalanus elongatus*) will have up to 4–5 generations per year requiring more flexibility in terms of achieving growth and reproduction over a wider range of temperatures.

Simulation studies have suggested that the larger Arctic copepods can reach diapause quicker and at earlier stages by utilising ice-algae early in the growth season (Ji et al. 2012), which is highly dependent on the phenological timing of the copepod. By contrast, the relationship between mean size and niche breadth breaks down for non-diapausing taxa due to the diminished role of seasonality for taxa of all sizes. Diapause life history strategies strongly structure the realised niche of copepods.

Comparing copepod niches across ocean basins

Our results show that for both the North Atlantic and Southern Ocean the most dominant variable defining a species niche is the SST, while the rank importance of the remaining variables differs between each region. For example, bathymetric depth has been shown to be a strong determinant of copepod habitats in the North Atlantic (Helaouët & Beau-grand 2007) and is evident here to be important in defining the copepod niches in this area. Species show an affinity for shallower shelf or deeper oceanic waters. In the Southern Ocean, depth has no significant role in defining niches because much of the area is oceanic (>500 m depth) with <1% of the area comprising shelf seas.

On average, we find that the realised niches of herbivores and omnivores are similar and are distinct from the realised niches of carnivorous copepods in both regions. However, we find that the differences between the regions are also reflected in the environmental variables that show separation of the realised niches of the different dietary strategies. The North Atlantic shows that herbivores and omnivores occur in significantly cooler, shallower waters of high productivity compared to carnivores, while in the Southern Ocean herbivores and omnivores occur in waters with significantly higher wind stress and productivity. In the Southern Ocean, herbivores and omnivores occur in areas of higher productivity compared with carnivores, but the mechanisms sustaining higher chl *a* differ from those in the North Atlantic. Wind-driven mixing creates enhanced regions of chl *a* (Carranza & Gille 2015) that benefit the herbivore and omnivore species.

A segregation in realised niches between herbivore/omnivore and carnivore functional groups similar to that found in the North Atlantic has been demonstrated along comparable environmental gradients in the Mediterranean (Benedetti et al. 2018). Carnivore functional groups were found to be dis-

tinct from the herbivores/omnivores, with carnivores found on average in significantly warmer and less productive areas. Findings in the open ocean have shown that carnivores tend to dominate in lower latitudes where productivity is low (Woodd-Walker et al. 2002), which benefits species that can prey on smaller copepods or gelatinous zooplankton (Takahashi et al. 2013). In contrast, herbivore/omnivore dietary strategies favour species that can adapt to seasonal variation in temperatures and productivity through lipid-storing and diapausing strategies when these are low (Barton et al. 2013b). In aggregate, these results from the North Atlantic, Mediterranean Sea, and Southern Ocean support the claim that functional traits, particularly dietary strategy, body size, and diapause structure the realised niche of copepods, although the realised niches are necessarily partially determined by the range of environmental conditions available. The robustness of these results helps anticipate the effects of climate change: trait-derived differences are likely to persist as environmental conditions change in any region of the ocean. Loss of any particular region of niche space from the environment will shift the niches of individual species, increase competition due to niche overlap, or lead to regional loss of species.

CONCLUSIONS

Our results indicate how traits including dietary strategy, body size, and life history strategies of copepods partially determine realised niches, indicating that these traits can be valuable information for predicting zooplankton biogeography and community changes in response to climate change. SST was the most important environmental variable structuring the realised niche across all dietary strategies in both oceans. Geographic differences in niches and the relative importance of variables defining the niche may limit the utility of regional species distribution models for extrapolating copepod biogeography over larger regions of the ocean. Similarities in niches and niche–trait relationships across the North Atlantic and the Southern Ocean indicate that further analysis of niches and their relationship to species' traits across wider geographic regions may illuminate robust relationships that can be used globally for projecting species biogeography.

Acknowledgements. We thank all the past and present staff and contributors of/to the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) who established and continue to

maintain the long-term CPR dataset and we thank the SCAR Southern Ocean CPR (SO-CPR) project for making their data publicly available. We thank anonymous reviewers for constructive feedback that has helped us improve the manuscript. We thank NSERC Canada (A.J.I., Z.V.F.), Canada Research Chairs program (Z.V.F.) and the National Science Foundation Biological Oceanography Program (grant number OCE-0962074) (N.R.) for their funding and support. This work was supported by a grant from the Simons Foundation (549935, A.J.I.; 549937 Z.V.F.).

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Editorial responsibility: Sigrún Jónasdóttir,
Charlottenlund, Denmark

Submitted: July 5, 2017; Accepted: June 6, 2018
Proofs received from author(s): July 20, 2018