

Patterns of abundance across geographical ranges as a predictor for responses to climate change: Evidence from UK rocky shores

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Abstract

Aim: Understanding patterns in the abundance of species across thermal ranges can give useful insights into the potential impacts of climate change. The abundant-centre hypothesis suggests that species will reach peak abundance at the centre of their thermal range where conditions are optimal, but evidence in support of this hypothesis is mixed and limited in geographical and taxonomic scope. We tested the applicability of the abundant-centre hypothesis across a range of intertidal organisms using a large, citizen science-generated data set.

Location: UK.

Methods: Species' abundance records were matched with their location within their thermal range. Patterns in abundance distribution for individual species, and across aggregated species abundances, were analysed using Kruskal–Wallis tests and quantile general additive models.

Results: Individually, invertebrate species showed increasing abundances in the cooler half of the thermal range and decreasing abundances in the warmer half of the thermal range. The overall shape for aggregated invertebrate species abundances reflected a broad peak, with a cool-skewed maximum abundance. Algal species showed little evidence for an abundant-centre distribution individually, but overall the aggregated species abundances suggested a hump-backed abundance distribution.

Delany and Burrows should be considered joint senior author.

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Main Conclusions: Our study follows others in showing mixed support for the abundant-centre hypothesis at an individual species level, but demonstrates an increased predictability in species responses when an aggregated overall response is considered.

KEYWORDS

abundant-centre hypothesis, algae, citizen science, intertidal, invertebrates, thermal niche

1 | INTRODUCTION

“Space for time” substitution (Blois, Williams, Fitzpatrick, Jackson, & Ferrier, 2013) suggests that patterns in species distributions across environmental gradients can give insights into the potential effects of climate change on species, communities and ecosystems (Hijmans & Graham, 2006; Walther et al., 2002). As such, an increasing number of studies have sought to understand general patterns in species abundances across ranges (Rivadeneira et al., 2010; Sagarin & Gaines, 2002a; Sagarin, Gaines, & Gaylord, 2006; Waldock, Stuart-Smith, Edgar, Bird, & Bates, 2019). One common hypothesis is that species are most abundant at the centre of their geographical or climatic range, known as the abundant-centre hypothesis (Brown, 1984; Whittaker, 1956). The abundant-centre hypothesis is a logical extension of niche theory (Holt, 2009) and is based on the assumption that environmental conditions at the centre of the species' range are optimal, and hence, the population reaches peak abundance and then declines towards the range edges (Brown, Stevens, & Kaufman, 1996; Whittaker, 1956). Generating evidence that either supports or rejects the abundant-centre hypothesis is crucial, as the hypothesis underpins a range of other ecological theories related to climate change (Sagarin et al., 2006). For example, it has been hypothesized that sites near range edges will see gradual population changes as the species range shifts with climate change (Helmuth, Mieszkowska, Moore, & Hawkins, 2006), but also that edge populations are more resilient to climate change as these populations are adapted to living on the edge of their tolerance (Hampe & Petit, 2005; Hewitt, 2004; Sagarin et al., 2006). Despite its importance, there remains a lack of evidence to support the generality of this hypothesis across habitats and ecosystems or that tests for the applicability of other distribution patterns.

Intertidal habitats provide an ideal system to investigate distribution-abundance patterns as they form thin stretches of discrete habitat that often extend over a latitudinal gradient (Rivadeneira et al., 2010; Sagarin & Gaines, 2002a; Sagarin et al., 2006). Although variation in local environmental conditions, such as wave exposure, topography and microclimate, may modify species distribution (Helmuth, Broitman, et al., 2006; Helmuth et al., 2002; Potter, Arthur Woods, & Pincebourde, 2013), broad latitudinal changes in species distributions as a result of climate change have been demonstrated (Hawkins et al., 2008; Mieszkowska et al., 2006; Poloczanska, Hobday, & Pitt, 2010). To date, evidence to support the abundant-centre hypothesis in intertidal species distributions is mixed and covers limited geographical areas. The abundant-centre

hypothesis has been shown to hold for some intertidal species, for example some species of porcelain crabs in Chile (Rivadeneira et al., 2010; Sagarin & Gaines, 2002a), but not for others, for example Pacific coast intertidal invertebrates (Sagarin & Gaines, 2002a). Other abundance distribution patterns may be present in some species, for example sporadic recruitment beyond limits of populations of adults may result in a long tail of low abundance (e.g. Schoeman et al., 2015). Alternatively, local environmental factors may outweigh broader biogeographic constraints on abundance leading to a uniform abundance distribution across the biogeographic range of a species (Sagarin et al., 2006), or different species may respond to different temperature metrics, such as maximum or minimum temperature (Seabra, Wetthey, Santos, & Lima, 2015). More recent work has highlighted the role of overlapping environmental and ecological conditions to form a mosaic of conditions that may disrupt any relationship between a single environmental variable, such as temperature, and abundance (Kroeker et al., 2016). As such, further work is needed in order to extend the scope of the evidence, both geographically and across a wider range of species.

Testing hypotheses relating to the impacts of climate change on species distributions requires comprehensive and comparable quantitative data sets across large geographical scales. Collecting this form of macro-ecological data using the resources available within the traditional research environment requires large investments of time and money (Parmesan, 2006). One alternative approach is to take advantage of the rise in popularity of citizen science (Kullenberg & Kasperowski, 2016). The ability of citizen science to generate large quantities of ecological data over broad spatial and temporal scales has been demonstrated repeatedly. For example, the eBird project has tested hypotheses related to changes in timing of spring bird migration through climate change (Sullivan et al., 2009), and a citizen science invasive species monitoring network robustly identified the distribution and abundance of an established invasive species (Delaney, Sperling, Adams, & Leung, 2008). Citizen science data have been used to investigate the abundant-centre hypothesis in only one habitat, that of shallow reef fish communities (Waldock et al., 2019), but not for any other habitat including the rocky intertidal. In this study, we use data generated through a UK national marine citizen science programme, Capturing our Coast (CoCoast), to test the applicability of the abundant-centre hypothesis, and other hypothesized distribution patterns, to a number of intertidal species of algae and invertebrates. Because the data only represent partial thermal ranges of individual species, we test individual assumptions of the abundant-centre hypothesis and its wider applicability across

groups of species. Specifically, we tested whether (a) individual species show increasing abundance trends in the cooler half of their thermal range and decreasing abundance trends across the warmer half of their thermal range, and (b) on average, aggregated species abundances conform to the abundant-centre hypothesis with peaks in abundance at the centre of the thermal range.

2 | DATA COLLECTION

Species distribution and abundance data were collected around the coastline of Britain by citizen scientists taking part in the CoCoast citizen science research programme. Citizen scientists underwent a 6–7 hr training programme that included both classroom and field sessions on intertidal survey techniques and species identification. A field protocol consisting of a horizontal 30 m transect within a single shore height (identified through biological zonation) was implemented using standardized equipment. Citizen scientists received field training on the specific methodology used in the surveys, including how to classify shore heights using biological zonation methods. Up to ten replicate 0.25 m² quadrats were placed randomly along the transect to maximize sampling efficiency (Miller & Ambrose, 2000; Pringle, 1984). Quantitative environmental data slope, substrate, percentage cover of bare rock, algal canopy, algal turf and other dominant space-occupying biota (barnacles/mussels) per unit area were also recorded. Each volunteer chose from one of fourteen distinct sets (“packages”) of 7–8 intertidal species to survey, resulting in records for 57 species. These species were surveyed at shore heights specified within the package, which represented the most suitable habitat for maximum abundance of each species. Each citizen scientist consistently used a single species package, except in instances where they had greater training and survey knowledge. The abundance of algae was estimated as percentage cover while invertebrate species were assessed as density. Citizen scientists had continued support from marine ecological experts throughout their involvement with the project through engagement events and field support sessions.

3 | DATA VERIFICATION

Data were screened for recorder errors in survey location, date and abundance values. Species distribution data were also checked against known species ranges using Marine Biological Association (MBA) and British Phycological Society (BPS) rulesets developed for National Biodiversity Network (NBN) Record Cleaner software. Where rulesets were not available, species ranges were generated from NBN Atlas verified species records and ranges were validated using MarClim papers and reports (Mieszkowska, 2017; Mieszkowska et al., 2005; Mieszkowska & Sugden, 2016) and expert knowledge from CoCoast researchers. Records of species that were rare, hard to identify or invasive were flagged for further investigation by local experts. Expert reviews of flagged records were

conducted by CoCoast staff, and citizen scientists were contacted with queries when required. Random spot checks of the data (every 1,000th record) were also checked for anomalies.

To understand misclassification rates, two techniques were used: an identification test ($n = 17$) using local samples of a subset of species and an online test using standardized photographs ($n = 83$). Citizen scientists across the UK were asked to participate in the tests alongside untrained members of the public. Analysis of the local samples identification tests suggests the mean correct identification rates for those species within the citizen scientists' chosen package were $84 \pm 3\%$ (mean \pm SE, Grist et al. 2019, unpublished data). Species with an overall mean correct identification rate of $<75\%$ from either test were discarded from the analysis, alongside morphologically similar species that were not included in the subset of species tested. To understand observer bias in percentage cover estimates, trained volunteers ($n = 30$) were asked to estimate percentage cover of algae in to-scale colour photographs. With an image of low algal cover (mean estimate of experts: 6%), citizen scientists overestimated cover by $3.3\% \pm 0.8$ (mean \pm SE). With an image of higher algal cover (mean estimate of experts: 54%), citizen scientists overestimated cover by $5.6\% \pm 1.6$.

4 | STATISTICAL ANALYSIS

After verification, 51 species remained totalling 187,661 observations at 1,053 locations around the UK regional seas. To reduce the influence of absences on the shape of abundance distribution patterns, and to avoid confounding occurrence with abundance, we constrained the number of absences in the data set following Waldock et al. (2019). Where absences outnumbered presences for a species, we randomly selected an equal number of absences to the presence records and bootstrapped the data 50 times. We then used the bootstrapped data set to calculate mean species abundance per location. Accuracy in location recorded varied between 10 s of metres and 10 km; therefore, records from replicate quadrats were grouped into 10 km grid squares and average abundance or percentage cover for each species was calculated per grid square providing average abundances for 244 coastal grid squares across the UK. Number of records per grid square per species varied from 2 to 44, with 3,740 average species abundances in total across all grid squares. Percentage cover and density data were analysed separately so as not to confound the different recording types.

The constrained geographical extent of the CoCoast programme did not allow the determination of abundance across the full extent of any species range. Thus to test individual assumptions of abundance distribution hypotheses, such as an increase in abundance in the cooler half of a species thermal range, required understanding of the relative position of a particular species record within its thermal range. This was achieved through a two-step process. Firstly, the 1982 to 2011 average sea surface temperature (SST) for each record was extracted from National Oceanic and Atmospheric Administration (NOAA) sea surface data annual averages

(0.25dg resolution, downloaded from <https://www.esrl.noaa.gov/psd/>) and extended to the coastline using 3 by 3 cell neighbour averaging (Reynolds et al., 2007). Records that extended into inlets and estuaries not covered by the NOAA data set were excluded from the analysis (49 records). Since minimum and maximum temperatures correlate strongly with annual mean temperature, and without knowledge of species-specific responses to seasonal minima and maxima (albeit important for individual species, Seabra et al., 2015), we used the mean temperature to identify overall response across species. To calculate the location of a record in the species thermal range, species thermal limits were obtained by matching global distributions from literature records to SST climatology (Burrows, 2019). Thermal range information was available for 29 of the 51 species present in the data set. Only these species were used in the subsequent analysis (2,153 records). We used temperatures at the edges of distributions (cold 10th percentile, T_{10} , warm 90th percentile, T_{90}) to define the thermal range of each species, without assuming that the optimum abundance would be at the centre. Range location (RL) was expressed as relative to these cool and warm bounds, from 0 at T_{10} (cool) to 1 at T_{90} (warm). Abundance was expected to decline as thermal range limits were approached (below T_{10} , $RL < 0$, and above T_{90} , $RL > 1$), but the trends in abundance within these bounds would show consistency or otherwise with the abundant-centre hypothesis. If individual species optima were randomly placed between limits, our analysis of multiple species patterns would result, on aggregate, in an average optimum temperature near the thermal range centre. However, any systematic deviation towards warm-skewed or cold-skewed distributions would result in a shifted peak of the aggregate species thermal abundance response. Local average annual SST (T) relative to species' T_{10} and T_{90} temperatures gave the thermal range location for each species record ($RL = (T - T_{10}) / (T_{90} - T_{10})$). Where there were no positive records of a species, likely owing to rarity of the species or lack of surveys in the preferred habitat of the species, linear models were excluded from subsequent analysis (4 brown algal species: *Alaria esculenta*, *Sargassum muticum*, *Bifurcaria bifurcata* and *Fucus distichus*).

To identify trends in abundance across the segment of the species' range spanned by the data, linear models of 10 km-gridded average logit (percentage cover) and log (density) data were fitted to the relative range location for each species. The slopes of the linear models of abundance with range location were extracted for each species and associated with the species' mean thermal range locations. To test the hypotheses that species will be increasing in abundance in a thermal range location of less than 0.5 and decreasing in abundance in a mean thermal range location greater than 0.5, Kruskal-Wallis tests were conducted on the individual species slopes for algal and invertebrate abundances, with mean range location as a factor (2 levels: >0.5 , <0.5).

To identify general patterns across all species, a general additive modelling approach was used to fit separate models for density of invertebrate species and percentage cover of algal species. Firstly, we standardized the data by scaling to one as the maximum abundance for each species in the data set. Different areas of the thermal

range of 0–1 were populated by scaled abundances from different species depending what part of the thermal niche for the species was sampled in the UK, with overlaps among species (see Figure 2). We then fitted thermal range location as a smooth term at the 75th and 95th quantiles of scaled abundance for algae and invertebrates in the R package “qgam.” This allowed us to model relationships between maximal abundances and thermal range, as opposed to mean abundances following standard modelling procedures. This method also does not require parametric distribution assumptions to be met (Fasiolo et al., 2019). Our models were fitted using cubic regression smoothing splines. Model fit was validated through residual and calibration plots. We assessed the quality of the smoothing term, thermal range location, at improving model fit by comparing the Akaike information criterion (AIC) of the full model and a null model with no explanatory terms. Only models where the addition of a thermal range location smoothing term improved model fit were interpreted. All analysis was conducted in the R platform for statistical computing (R Development Core Team, 2011).

5 | RESULTS

Across the sections of the range contained within the data set, the slope of individual invertebrate species density was significantly different if the mean thermal range location was in the warmer half of the range, compared to the cooler half of the range. Species recorded in the cooler half of the range had more positive slope and species recorded in the warmer half of the range had more negative slope ($\chi^2 = 4.667$, $df = 1$, $p = .031$, Figure 1a). This suggests that thermal range location may have an effect on trends in abundance for individual invertebrate species on UK coasts. There was no significant difference in the slope of the abundance of algal species regardless of whether the mean range location present in the data set was in the colder or warmer half of the range ($\chi^2 = 1.114$, $df = 1$, $p = .291$, Figure 1b).

For the 75th percentile of abundance for invertebrate species, abundance was higher in the central portion (range location 0.1–0.7) with apparent peaks in abundance in both the cooler and warmer areas of the thermal range (e.d.f. = 7.67, $\Delta AIC = -514.5$, Figure 2a). Thermal range location explained 11.3% of the deviance in abundance. Thermal range location explained 52.3% of the model deviance in abundance at the 95th percentile of abundance for invertebrates (e.d.f. = 3.625, $\Delta AIC = -1014.2$, Figure 2a). The improvement in fit shown by the more complex relationship at the 75th percentile is unlikely to be meaningful. No single species spanned the full range of thermal range locations, so the multimodal nature of the relationship more likely reflects the summation of multiple, different-shaped abundance temperature curves. At the 95th percentile, scaled abundance aggregated across multiple invertebrate species showed a broad peak, where the maximum abundance peak was closer to the cool edge of the thermal range. For scaled abundance aggregated across algal species, thermal range location improved model fit for the 75th percentile of abundance (e.d.f. = 4.99,

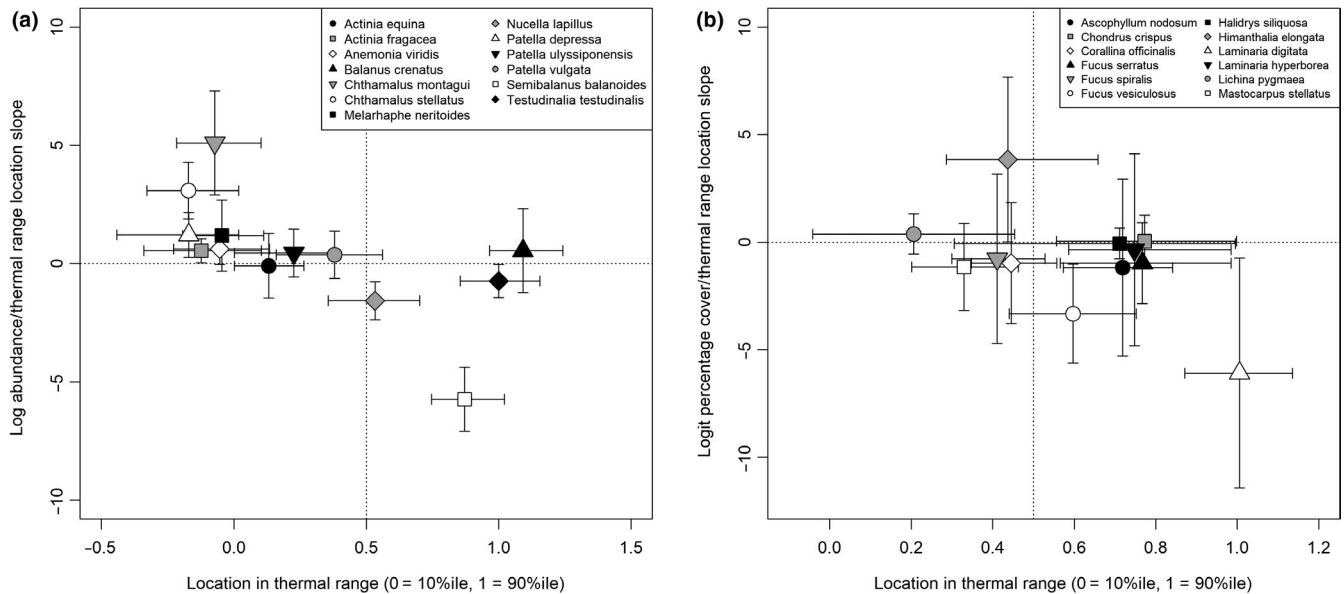


FIGURE 1 Slope of linear models of abundance against mean thermal range location contained within the data for (a) invertebrate species; (b) algal species. Vertical error bars represent standard error around the estimated slope. Horizontal bars represent the minimum and maximum thermal range location contained within the data set

Δ AIC = -300.42, Figure 2b) and explained 6.73% of the deviation in algal abundance. Algal abundance showed alignment with a hump-shaped distribution at the 75th percentile. However, at the 95th percentile, the addition of a thermal range location term to the null model did not improve model fit (e.d.f. = 3.205, Δ AIC = +192.43).

6 | DISCUSSION

Our study supports idiosyncratic individual species abundance patterns across sections of thermal ranges of intertidal organisms occurring in the UK, yet when abundances are aggregated across species, with the inherent caveats of that approach, there is supporting evidence for a central peak in abundance in algal species, but a broader one for invertebrate species. Although this hump-shaped distribution was evident for the 75th percentile of the algal abundances, there was no evidence for thermal range location limiting the absolute maximum abundance of algal species. This suggests that populations of algae are patchier at the site scale towards range edges, with high, space-limited abundance in occupied areas and low elsewhere, giving a consistent upper limit to abundance across the thermal range. For invertebrates, especially mobile ones, population density may vary more smoothly between favourable within-range and unfavourable marginal locations. Furthermore, across invertebrate species, our data suggest a relationship between abundance and thermal range location other than a simple unimodal abundant-centre distribution. This study provides additional evidence that the abundant-centre hypothesis is not a universal paradigm for individual species as each species response to thermal environment may be idiosyncratic. However, our data suggest we may be able to predict average species behaviour in response to changes in the thermal

environment, and for some guilds of species this could conform to an abundant-centre distribution.

Our results support a growing acknowledgement that many individual species have idiosyncratic responses to their thermal environment (Sagarin & Gaines, 2002b). Hence, the abundant-centre distribution hypothesis may reflect an oversimplification of species abundances across ranges when considering individual species distribution patterns (Dallas, Decker, & Hastings, 2017; Sagarin & Gaines, 2002b). Although our data do not reflect the full thermal range for each of the individual species investigated, it does contain a full range of thermal niche locations across all species. As such, if the abundant-centre hypothesis was universal for all species, we would expect to see consistent increasing abundance trends in the cooler half of the range, and decreasing abundance trends in the warmer half of the range for each species, with no deviation from these patterns across all species studied (Sagarin et al., 2006). However, although we found some evidence to support this assumption in invertebrate species, algal species abundance trends did not follow this pattern. Previous studies of intertidal organisms have identified a number of local environmental conditions that may disrupt any potential latitudinal or distance driven patterns in the abundance (Helmuth et al., 2002). These include wave action, local climate patterns and timing of the tidal cycle, all of which may lead to mosaics in the thermal environment that provide greater thermal variation over a small scale than seen on average over a latitudinal scale as investigated here (Denny, Dowd, Bilir, & Mach, 2011; Helmuth, Broitman, et al., 2006). Individual species may also respond differently to different metrics of the thermal environment, and thus, any single metric may not be sufficient to test for the abundant-centre hypotheses across species as it may not allow disentanglement of optimum thermal environment from the metric that best describes the optimum for

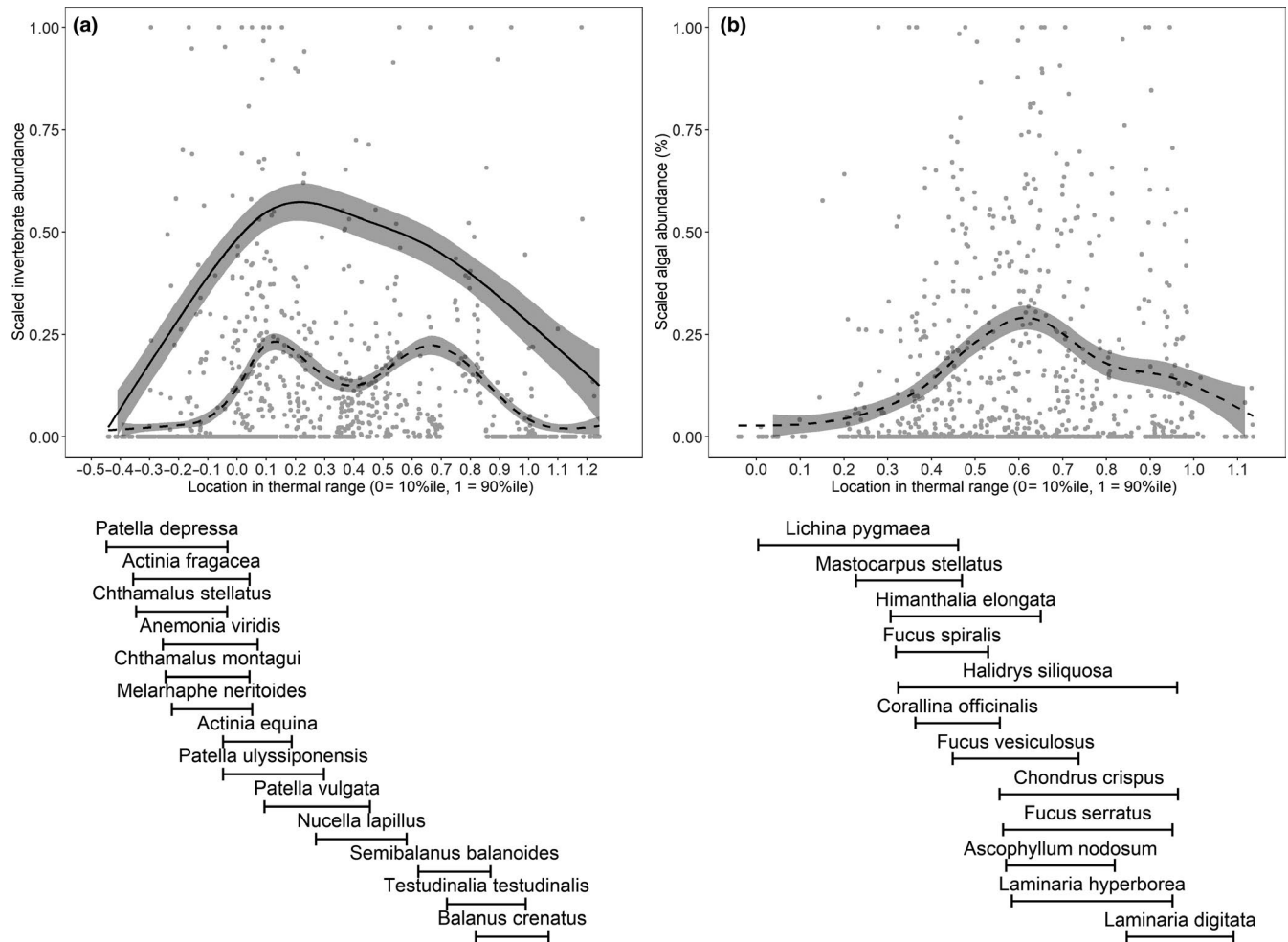


FIGURE 2 Scaled species abundance across thermal range for (a) invertebrate species (%) and (b) algal species (density). Small points are individual species abundances. Model fits are quantile general additive models with standard errors. Solid line is the 95th percentile model fit, and dashed line is the 75th percentile model fit. Grey dots are the scaled abundance of species. The lines beneath the plot show which species are represented in grey dots in each part of the thermal range, starting at the coolest part of the range sampled and ending at the warmest part of the range sampled

each species (Seabra et al., 2015). Furthermore, complex interactive effects of local environmental conditions with species life histories and species interactions may lead to unexpected patterns in abundances, that do not align with simple distance-abundance models, such as the abundant-centre hypothesis (Bas, Luppi, & Spivak, 2005; Gilman, 2005). For example, a study in the Northwest Atlantic found intertidal mussel abundance to be negatively associated with the critical aerial exposure time, whereas dogwhelk abundance was positively correlated with mussel abundance, leading to a complex effect of both the local environmental conditions and species interactions (Tam & Scrosati, 2011). Because our study is limited by the range of thermal niches sampled, we cannot disregard the abundant-centre hypothesis universally for all species. However, our results further suggest that some individual species responses to the thermal environment may be idiosyncratic and highly variable across their ranges, disrupted by local environmental factors.

Here, we provide evidence that the abundant-centre distribution may hold, on average, across an assemblage of species, even where

it fails at the scale of individual species. At smaller scales generalizations can be harder to tease out because local variation masks patterns (Lawton, 1999), whereas this influence of local variation contracts at larger scales, facilitating identification of patterns. Our results follow a recent study on reef fish (Waldock et al., 2019) to provide evidence to support a hump-backed distribution in algal species when looking at aggregated species responses, with the peak falling close to the centre of the thermal range. One potential reason for this result could be that the cold-water boreal algal species included in this study could simply grow to larger sizes in the colder northern latitudes, but not necessarily increase in abundance of plants. Another potential reason as to why algal species may conform to an abundant-centre distribution, or another distance-abundance relationship, may be owing to their lack of mobility. Algal species, and other sessile organisms, are unable to move to avoid local unfavourable microclimatic conditions. Therefore, if settlement does not occur within a local thermal refuge, such as a shaded area, survival is unlikely. Hence, abundance patterns of these sessile

species may be more strongly linked to environmental conditions, such as temperature, than mobile species that can better ameliorate environmental conditions by using refugia on the shore (Denny et al., 2011). Thermal range location did not influence the absolute maximum abundance of algal species in our analysis, suggesting that habitat availability and other factors may be more influential in determining maximum abundances.

Our results provided some evidence of individual invertebrate species increasing in abundance in the cool half of their range and decreasing in the warm half; yet scaled up to look across all invertebrate species in our data set, the data do not support the abundant-centre distribution across all levels of abundance. Interestingly, the relationship between abundance and thermal environment was more complex, displaying a dip in abundance in the centre of the thermal range within the 75th percentile. If such a dip is not an artefact of aggregating multiple species data, there could be a greater influence of negative intraspecific interactions in the centre of the thermal range (Maestre, Callaway, Valladares, & Lortie, 2009), which may propagate up to influence larger macro-ecological patterns. Our data set contains several species that have well-documented density-dependent control of population size, such as barnacles (Bertness, 1989; Jenkins, Murua, & Burrows, 2008). Alternatively, a dip in abundance at the thermal optima could reflect an "ideal despotic distribution," where optimal habitats are monopolized by relatively few species (Fretwell, 1972). At the 95th percentile, our data support a broader peak. This difference in abundance distribution between the 75th and 95th percentiles could be explained by absolute maximum abundance of invertebrate species being determined by temperature alone, as opposed to at the 75th percentile where environmental mosaics may be more important in determining abundances. The skewed maximum abundance peak at the 95th percentile could also be an artefact of the leading edge of the northern range for a number of the sampled species, such as *Patella depressa* occurring at the biogeographic breakpoint between Boreal and Lusitanian waters that bisects the UK, and therefore, oversampling at this range edge has led to a cool-skewed average distribution. Previous studies have emphasized the importance of sampling along the full thermal range, where possible, in order to increase confidence in any abundance distribution patterns seen (Sagarin & Gaines, 2002b).

This study further upholds the well-documented value of engaging members of the public in scientific pursuit, specifically demonstrating here the capability of volunteers to generate data that can test broad macro-ecological theories. Citizen science approaches are most optimally deployed in cases where teams of professional scientists would otherwise struggle on capacity grounds to attain the required spatial and temporal scales of data collection (Garcia-Soto et al., 2017; Hyder, Townhill, Anderson, Delany, & Pinnegar, 2015). Such data have been used to examine range shifts in birds, distribution of invasive species and the shifting of phenology, but has rarely been used to identify patterns in abundances across large scales (Dickinson, Zuckerberg, & Bonter, 2010). Our results show that through appropriate design, methodology and training, citizen scientists can generate detailed quantitative data that can go beyond

presence/absence or phenological questions and test for patterns in abundance across ranges and across a broad array of species. This study additionally contributes to the growing evidence of the efficacy of citizen science to yield valuable data in marine environmental contexts (Thiel et al., 2014), which is disproportionately underrepresented compared to terrestrial studies (Cigliano et al., 2015; Roy, Pocock, Preston, Roy, & Savage, 2012). Given the scale of environmental threat, and the resource-strapped challenges to meet necessary knowledge gaps and address climate change-related theories, citizen science approaches should increasingly be considered to achieve positive outcomes for science and for the marine environment (Bonney et al., 2014; Garcia-Soto et al., 2017; Hyder et al., 2015).

To conclude, we found further evidence for idiosyncratic abundance distribution patterns across species thermal ranges when considering individual species. However, we provide further support for increased predictability in species responses at the larger scale of assemblages and communities, and evidence that some guilds of species may overall show a unimodal abundance distribution.

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DATA AVAILABILITY STATEMENT

The data used in this manuscript can be found on the National Biodiversity Network Atlas: <https://registry.nbnatlas.org/public/show/dr2247>.

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