



Episodic and non-uniform shifts of thermal habitats in a warming ocean



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ABSTRACT

Ocean temperatures have warmed in most regions over the last century and are expected to warm at a faster rate in the future. Consistent with the view that marine species are thermally constrained, there is growing evidence that many marine species have already undergone poleward range shifts in line with warming trends. This study uses historical observations of ocean temperature and climate model projections to examine the movement of isotherms that mark the boundaries for species' thermal habitats. In particular, we compare the rates of isotherm movement between different ocean regions and at different time scales and examine to what extent the implied movement is uniform or sporadic. Widespread long-term warming implies poleward shifts of isotherms in almost all regions. However, as the speed of isotherm movement is inversely related to local meridional SST gradients and the pattern of ocean warming is heterogeneous, speeds vary considerably between regions, season and over time. At present on decadal and longer timescales, changes due to low frequency natural SST variability can dominate over human-induced changes. As such, there are multidecadal periods in certain regions when we would expect to see range shifts that are much faster or in the opposite direction to that implied by a monotonic warming. Based on central estimates from the latest suite of climate model projections, median isotherm speeds will be about seven times faster in the 21st century compared to the 20th century under *business as usual* emissions. Moreover, SST warming is projected to be greater in summer than in winter in most oceanic regions, contrary to what is projected to occur over land. As such net poleward isotherm speeds, particularly in the northern hemisphere summer, are projected to be considerably faster than in winter. Finally we show that isotherms can exhibit erratic migration rates over time, even under uniform warming. Isotherm movement tends to stall at thermal fronts for extended periods of time and then rapidly shift to a new position, marked by more poleward fronts. This implies that species ranges would also be expected to undergo sudden rapid shifts rather than exhibiting a gradual monotonic poleward march.

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1. Introduction

All species or populations within a species have an optimal temperature range in which they function most efficiently (Drinkwater et al., 2010; Huey and Kingsolver, 1989). Temperature strongly influences biological processes such as temporal patterns of growth, survival or reproduction, as well as spatial patterns of body size and population density (Angilletta, 2009). Move too far outside a species' optimal range and its ability to function degrades to a point where the population is no longer viable.

Consequently, temperature is often an important factor in determining the geographical distribution of a species. This is particularly pertinent for marine species as they are typically more constrained by thermal limits than terrestrial species (Sunday et al., 2012). In the marine environment, temperature is tightly linked to the capacity of species to perform aerobically (Pörtner, 2002), and organisms living in temperatures outside their thermal optima experience reduced aerobic scope, which negatively affects their performance and ultimately reduces their abundance (Pörtner and Knust, 2007). Hence, where there are long-term changes in the temperature of a region, for example driven by anthropogenic climate change, a species population may be able to tolerate the higher temperature, but this may come at the cost of reduced efficiency (Drinkwater et al., 2010 and references therein);

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the species population may move to a region with more favourable temperatures, or the species population may become extinct. Even where a species population can adapt to temperature changes, indirect effects may adversely affect the population (e.g. Walther, 2010). New predator species may enter the region, existing prey species may migrate away, the timing or phenology of predator-prey interactions may change or other physical or biogeochemical changes may occur (e.g. changes in stratification, circulation or nutrient supply).

Over the last century, increased radiative forcing, driven primarily by rising concentrations of greenhouse gases, have resulted in a clear large-scale warming of the earth surface including the upper ocean (IPCC, 2013). Given that emissions of greenhouse gases are still accelerating (e.g. Raupach et al., 2007; Le Quere et al., 2013) further warming, at faster rates, is expected. In conjunction with a large equator-to-pole temperature difference, such broad scale, long-term warming will in most regions cause a poleward movement of *thermally bound habitats*, the region between two isotherms that border a species thermal range.

For terrestrial systems there is a large body of evidence for thermally driven species migrations. For example Chen et al. (2011) performed a meta analysis of the literature with regard to terrestrial range shifts. Based on a sample of over 700 species from multiple taxa they found median polewards range shift speeds of ~17 km/decade. They also showed a significant correlation between the rate of range shift for species and the associated rate of regional warming. Moreover, the correlation was increased when this observed rate was compared with the theoretical rate of isotherm speeds based on both the local rate of warming and regional differences in temperature gradients (see below). While the evidence for species range shifts in the marine environment is comparatively more limited, there is nevertheless compelling evidence of a predominance of poleward range shifts (Nye et al., 2009; Perry et al., 2005a; Przeslawski et al., 2012; Wernberg et al., 2011). For example, a meta analysis by Sorte et al. (2010) found a poleward migration in 75% of the ($n=129$) species (including primary producers, fish, molluscs, crustaceans, birds, cnidarians and sponges) for which there was evidence of a range shift. This is already having a measurable impact on world fisheries, resulting in a global 'tropicalisation' of catch, i.e. an increasing dominance of warm-water species (Cheung et al., 2013).

In this study we examine long-term observed surface isotherm speeds in relation to spatial differences in meridional SST gradients (Section 3.1) and contrast this with speeds calculated on decadal timescales at which natural variability dominates over anthropogenic changes (Section 3.2). We then examine projections of isotherm speeds based on the latest generation of climate models (Section 3.3), for the annual mean and for summer and winter seasons (Section 3.4) and investigate characteristics of the temporal evolution of isotherm locations subject to large inter-annual variability and in regions of very different background spatial gradients (Section 3.5). Finally we briefly examine an alternative adaptation strategy available to some species: vertical migration to greater depth (Section 3.6). Implications for marine species of these physical environmental changes and key recommendations are provided in Section 4.

2. Methods

Population distributions are set by a variety of physical and biogeochemical factors that define habitat suitability as well as food availability and pressures associated with predators and fishing. One of the primary abiotic constraints, however, is ocean temperature. Ocean temperature is a well understood variable that has been routinely measured, particularly in the upper ocean, over

Table 1
CMIP5 models used for projections.

SST	Subsurface temperatures
ACCESS1-0	ACCESS1-0
ACCESS1-3	ACCESS1-3
CCSM4	CCSM4
CESM1-CAM5	
CESM1-WACCM	
CNRM-CM5	CNRM-CM5
CSIRO-Mk3-6-0	CSIRO-Mk3-6-0
CanESM2	CanESM2
FIO-ESM	
GFDL-CM3	
GFDL-ESM2G	
GFDL-ESM2M	
GISS-E2-R	GISS-E2-R
HadGEM2-AO	
HadGEM2-CC	HadGEM2-CC
HadGEM2-ES	HadGEM2-ES
IPSL-CM5A-LR	IPSL-CM5A-LR
IPSL-CM5A-MR	
IPSL-CM5B-LR	
MIROC-ESM-CHEM	MIROC-ESM
MIROC5	MIROC-ESM-CHEM
MPI-ESM-LR	MPI-ESM-LR
MRI-CGCM3	MRI-CGCM3
NorESM1-M	NorESM1-M
NorESM1-ME	
bcc-csm1-1	bcc-csm1-1
inmcm4	inmcm4

long periods of time. Moreover, climate models are able to simulate the future evolution of SST with a relatively high degree of confidence (IPCC, 2013) compared to many other physical or biogeochemical characteristics of the ocean. Here we examine observed and simulated surface and subsurface ocean temperature over the historical period and projected temperature using the most recent generation of coupled ocean-atmosphere climate models. We aim to provide insights into the evolution of isotherms and by association thermally bound habitats in an ocean subject to long term warming, strong interannual to multidecadal variability and large spatial heterogeneity.

The historical SST observations are based on the HadISST gridded dataset (Rayner et al., 2003). This provides spatially complete SST estimates at a $1^\circ \times 1^\circ$ resolution from 1871 to the present day, using in situ observations prior to 1981, and combining in-situ and satellite data thereafter. While in most regions centennial trend estimates are similar using different datasets, there is increased uncertainty particularly at high latitudes and in the tropical Pacific, where in-situ observations in the earlier part of the 20th century are sparse (Deser et al., 2010).

Historical simulations and future projections of surface and subsurface temperature are obtained from the state-of-the-art climate models taking part in the Coupled Model Intercomparison Project phase 5 (CMIP5, Taylor et al., 2012). Historical simulations are generally forced by observations of greenhouse gases, aerosols, ozone and insolation, from approximately 1850 to 2005. To examine future changes, we use simulations that follow the RCP85 emissions pathway (Riahi et al., 2007). This can be considered as a 'business as usual' scenario in which greenhouse gas emissions remain large over the 21st century reaching ~1370 CO₂-equiv. in 2100 (Moss et al., 2010). The RCP85 scenario has been chosen here (rather than one of the lower emissions pathways) as there is a large amount of model data available for this scenario. It also offers the largest (climate change) signal to (internal variability) noise ratio, making this scenario particularly useful for identifying robust climate change patterns. We would expect similar results for lower emissions scenarios but

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