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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.

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 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.

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
MIROC-ESM-CHEM	MIROC-ESM-CHEM
MIROC5	
MPI-ESM-LR	MPI-ESM-LR
MRI-CGCM3	MRI-CGCM3
NorESM1-M	NorESM1-M
NorESM1-ME	
bcc-csm1-1	bcc-csm1-1
inmcm4	inmcm4

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 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 CO_2-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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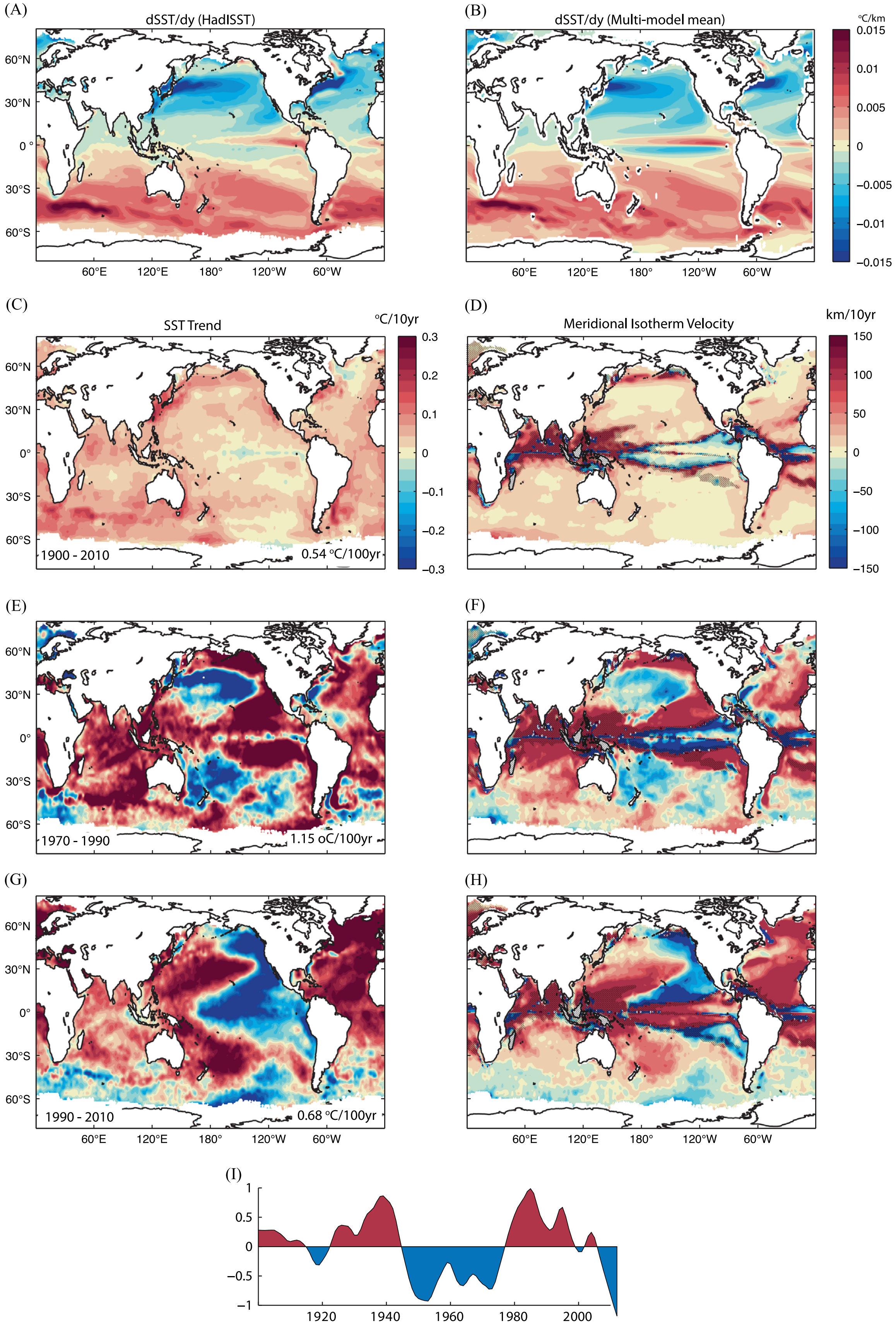

Fig. 1. Long-term mean meridional SST gradients based on (A) HadISST observations and (B) the multi-model mean. (C) Observed linear warming trends and (D) the associated isotherm migration speeds for the 1900 to 2010 period (where red/blue colours denote poleward/equatorward migration. (E) And (F) are the same as (C) and (D) for the 1970–1990 (positive PDO transition) period. (G) And (H) are the same as (C) and (D) for the 1990–2010 (negative PDO transition) period. (G) Smoothed PDO index (http://jisao.washington.edu/pdo/PDO.latest). Colour bars are the same for panels C, E and G and for panels D, F and H. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

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with correspondingly weaker projected warming and poleward isotherm speeds. For SST projections we use output from 27 different climate models, while for the subsurface projections we use output from 17 models, based on data availability (see Table 1).

In the absence of other factors, we would expect range shifts of thermally sensitive species to be influenced by shifts in the location of isotherms that mark species′ thermal limits. We follow the method of Loarie et al. (2009) and Burrows et al. (2011) to estimate the temporally-averaged north–south isotherm speeds at a certain location ($\bar{v}$). We calculate the ratio of the local temperature change (calculated as a SST trend, from observations or climate models, over the desired averaging period) to the local meridional SST gradient (calculated using SST observations over a 1980–2010 reference period):

$$\bar{v} = \overline{\left(\frac{\partial y}{\partial t}\right)} = \overline{\left(\frac{\partial SST}{\partial t}\right)} / \overline{\overline{\left(\frac{\partial SST}{\partial y}\right)}} \qquad (1)$$

where y is the latitude of a given isotherm and the overbar indicates averaging over the time period under consideration. The double overbar indicates averaging over the 1980–2010 reference period using HadISST; we use the observed meridional SST gradient over a period of good observational coverage to take account of biases in the mean state of climate models. As this reference gradient is also used when examining projected changes, our projections assume that the meridional SST gradient does not change substantially in the future. As such, the speeds calculated with Eq. (1) are an approximation as both the instantaneous rate of change of SST and the instantaneous SST gradient vary with time. A sensitivity analysis demonstrates that our results are relatively insensitive to the use of observed versus simulated multi-model mean meridional SST gradients, as the multi-model mean gradients closely match the observed gradients in most locations (Fig. 1A and B; although larger biases are evident for individual models). Moreover we compared isotherm speeds using the multi-model mean SST gradients calculated from the historical simulations, from 1980 to 2010 and the RCP85 projections, from 2070 to 2100 (Figure not shown). Differences are relatively minor over most of the domain, indicating that the use of a constant SST gradient is an acceptable approximation when examining large-scale patterns. Indeed these differences are considerably smaller than differences between speeds calculated using observed versus multi-model mean SST gradients.

Isotherm speeds and locations are calculated on annually averaged, annual maximum and annual minimum temperatures (derived from monthly observational or climate model data). Annual maximum or minimum temperatures generally correspond to climatological maximum summer and minimum winter temperatures, except at low latitudes where the seasonal cycle is poorly defined. For the calculation of annual maximum or minimum isotherm speeds we use meridional SST gradients calculated from observed annual maximum or minimum temperatures, respectively.

3. Results

3.1. *Historical long-term, isotherm speeds*

Meridional gradients in long-term mean SST show monotonically decreasing temperatures from the equator to the poles for most oceanic regions (Fig. 1A). The most prominent exception to this is in the equatorial central and eastern Pacific and Atlantic basins where the prevailing equatorial Trade Winds drive an upwelling of relatively cool water and as such equatorial waters have lower SST than off the equator. Strong regional spatial differences exist in the meridional SST gradients, with the strongest gradients along the fronts associated with western boundary current extensions and the Antarctic Circumpolar Current.

The speed with which isotherms at a certain location move poleward depends on both the local rate of change of SST and the local meridional gradient in SST (Eq. (1)). Given the broad-scale poleward gradient and the consistent centennial warming, isotherms at almost all locations averaged over the last century, have moved poleward (Fig. 1D; the main exceptions being the parts of the tropical ocean where the local SST increases towards the poles). However, large spatial differences are apparent. At low latitudes, where SST gradients tend to be weak, speeds with which isotherms move poleward tend to be larger. Interestingly, many of the regions of enhanced warming, such as the Southern Ocean and the extensions of the Western Boundary Currents, are not associated with particularly large speeds as meridional SST gradients in these regions (i.e. the denominator in Eq. (1)) are also large. Overall, based on all ocean regions the median isotherm speed is ~13 km/decade (Fig. 2A; ~6 to ~27 km/decade interquartile range).

Based on the multi-model mean estimate of historical warming from the climate models, simulated isotherm speeds are in general slower than observed (median ~9 km/decade). This is a result of a smaller estimate of globally averaged SST warming in the climate models compared to the warming derived from HadISST (0.041 °C/decade for the multi-model mean versus 0.054 °C/decade for HadISST, Fig. 2C). The estimated speeds are relatively insensitive to whether we use the observed or multi-model mean meridional SST gradient (on the denominator of Eq. (1)) to calculate speeds (Fig. 2A).

3.2. *Multidecadal variability in isotherm speeds*

For most biological applications, decadal and multidecadal time scales are more relevant than centennial ones. While some observational time-series of marine populations cover centennial timescales (generally associated with economically important species; Cheung et al., 2009; Sorte et al., 2010), most biological time series are much shorter. On the timescale of a few decades, natural variability in regional SST will dominate over any long-term trend associated with systematic increases in greenhouse gas concentrations (e.g. Tebaldi and Knutti, 2007), although the relative importance of greenhouse-induced changes will likely increase in the future.

Fig. 1E and G shows observed SST trends over two different 20-years periods (1970–1990) and (1990–2010); the globally averaged trends for these two periods are ~0.12 °C/decade and ~0.07 °C/decade, respectively, consistent with a faster rate of global warming over recent decades (20th century trend: ~0.054 °C/decade). The trends are highly spatially heterogeneous compared to the centennial scale trend (Fig. 1C), with both warming and cooling trend magnitudes exceeding 0.6 °C/decade in some regions. Moreover, across extended regions the trend changes direction between the two periods. For example, there is a strong warming in the central and eastern tropical Pacific and northeastern Pacific, flanked by cooling further west in the early period. This pattern reverses sign in the later period. This ENSO-like SST pattern is characteristic of the low-frequency Pacific Decadal Oscillation (PDO; e.g. Mantua and Hare, 2002)/Interdecadal Pacific Oscillation (IPO; e.g. Power et al., 1999). Indeed, over the 1970–1990 period the PDO index was transitioning from a negative to positive state, while there was a negative transition between 1990 and 2010 (Fig. 1I). Associated with the regional changes in SST trends are collocated changes in isotherm speeds. For example along the coast of California isotherms migrated polewards, averaged over the 1970–1990 period but moved equatorwards over the 1990–2010 period. Thus, we would expect a equatorwards migration of certain thermally sensitive species in this region over the most recent 20 years, opposite to the direction that long-term warming

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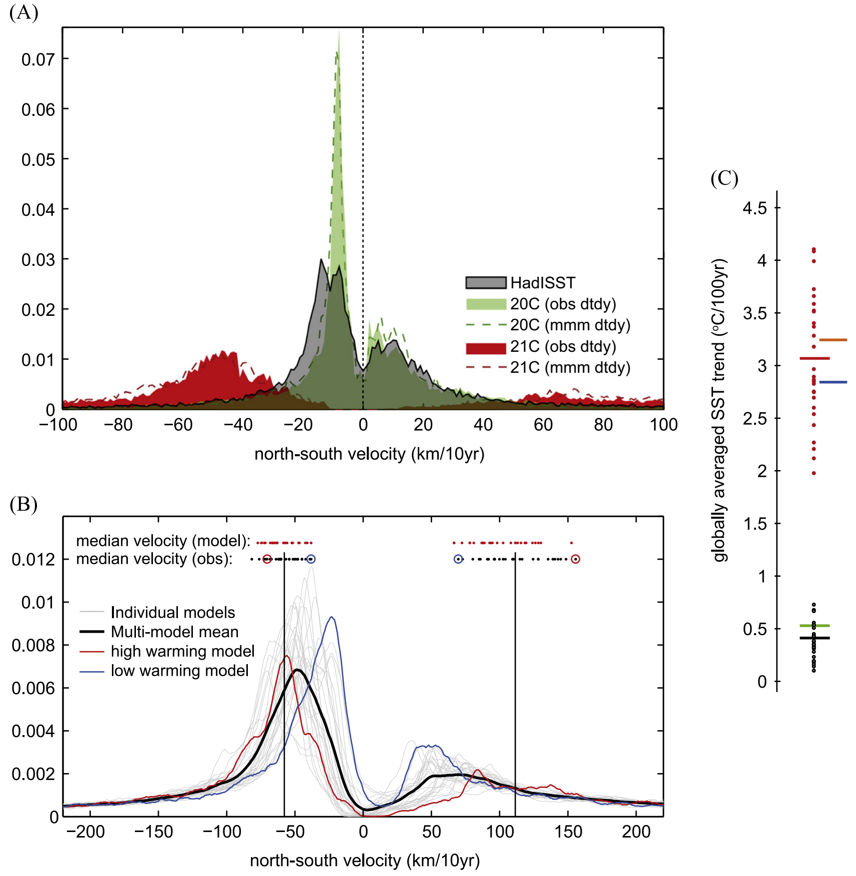

Fig. 2. (A) Area weighted frequency distribution of north–south temporally averaged isotherm speeds for the historical period (1900–2010 HadISST: grey, 1900–2005 multi-model mean: green) and projection period 2005–2100 (red). Shaded distributions are calculated using the observed meridional SST gradient (dashed lines indicate associated distributions calculated using the multi-model mean SST gradient). All distributions are defined to have an area of 1. (B) As (A) but for projected distributions only. Grey lines represent distributions for individual models, thick black line is the multi-model mean and the red and blue curves show two selected models with relatively high (red) and low (blue) isotherm speeds. Closed circles above the curves indicate the median northward and southward speeds calculated using the observed (black) or individual model (red) SST gradients; open red and blue circles are the median for the high and low velocity models, respectively; vertical lines are the median northern and southern hemisphere speeds (based on multi-model mean warming and the observed SST gradients). (C) Globally averaged rate of warming for individual models (1900–2005, historical simulation: black circles; 2005–2100, rcp85 as red circles); black and red horizontal lines are the associated multi-model mean warming trend and the green horizontal line is the observed 1900–2005 trend; horizontal orange and blue lines indicate multi-model mean globally averaged trends based on annual maximum and minimum SST, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

would imply. Indeed, many oceanic fishes in the southern California region alternate in abundance and distribution depending on the dominance of multidecadal periods of either warm- or cold water (Anthony Koslow et al., 2013; Hsieh et al., 2009).

3.3. Long-term climate model projections

Over the 21st century the multi-model mean projected warming rate is ~7 times faster than for the 20th century under the RCP85 scenario (Fig. 2C; inter-quartile range across the different models of 5 to 12x faster). Despite spatially uniform increases in greenhouse gases, distinct regional differences in warming rate become clear (Fig. 3A). As noted for the historical trends, certain regions associated with western boundary currents or their extensions exhibit enhanced warming. While in other regions, such as the Southern Ocean, warming is relatively weak. This was also found for the CMIP3 models and is consistent with the projected intensification of the surface westerlies and an associated increase in northward Ekman transport of cold high latitude waters (Sen Gupta et al., 2009). There is also a strong hemispheric asymmetry in warming particularly in the Pacific and Indian basins, largely associated with differences in projected wind changes and associated changes in evaporative ocean cooling. For example the projected intensification of the south-easterly trade winds results in relatively weak warming in the south-eastern Pacific, while the relatively strong warming along the equator and the northern Pacific is associated with a weakening of the north-easterly and equatorial Trade Winds (Timmermann et al., 2010; Xie et al., 2010).

Given the projected acceleration of warming across the oceans, projected poleward isotherm speeds are correspondingly faster (Figs. 2B and3B). Based on the multi-model mean warming trend, median speeds for the 21st century are ~70 km/decade (~42 to ~180 km/decade inter quartile range) under RCP85, although modal (most frequently simulated) speeds are considerably lower as a result of the long tail of high isotherm speeds. Regional differences in speeds generally have a similar spatial signature to those found for the historical period, albeit considerably amplified, as these are largely determined by the spatial differences in meridional SST gradients.

A distinct northern/southern hemisphere asymmetry exists in the magnitude of isotherm speeds. This is apparent for both historical and future isotherm movement, although much clearer for the projections. The median projected isotherm speed in the southern hemisphere is ~57 km/decade (~41 to ~120 km/decade inter quartile range) compared to ~111 km/decade (~55 to ~266 km/decade) in the northern hemisphere, under RCP85 (Fig. 2B; positive/negative speeds are primarily from the northern/southern hemisphere). This is partly due to the enhanced warming projected in the northern hemisphere compared to the southern hemisphere: the hemisphere-averaged

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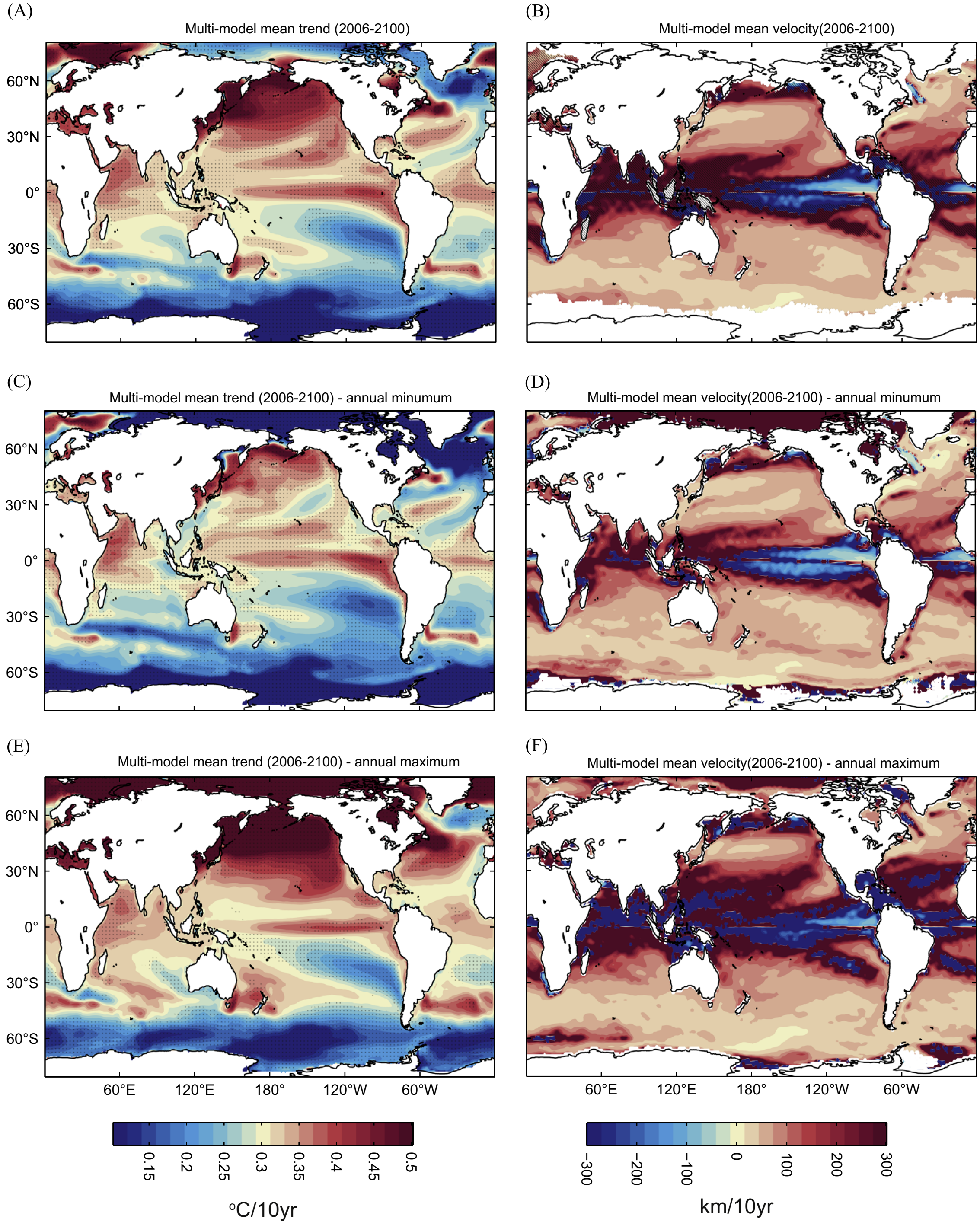

Fig. 3. (A) Multi-model mean linear trend in SST based on RCP85 scenario; (B) average (2006–2100) projected meridional isotherm velocity calculated using Eq. (1). C And D (E and F) same as A and B but using annual minimum (maximum) SST. Mottling on trends maps (A, C and E) indicate regions where at least 75% of models agree that the warming will be faster or slower than the global mean.

warming is ~0.5 C/100 yr faster in the northern hemisphere (Fig. 2C). More important however is that meridional gradients generally tend to be weaker in the northern hemisphere, leading to larger isotherm speeds.

The results presented above are based on the mean warming across 27 different climate models (Table 1). It should be acknowledged, however, that there is a considerable spread in the pattern and strength of warming across different models and associated isotherm speeds. Rates of globally averaged SST warming over the 21st century, under RCP85, range from ~2 °C to ~4 °C (Fig. 2C). This corresponds to a range in median speeds across different climate models of ~38 to ~82 km/decade in the southern hemisphere and ~70 to ~156 km/decade in the northern hemisphere (Fig. 2B). That is, even if we had perfect knowledge of future CO_2 concentrations we would still have more than a factor of two uncertainty in isotherm speeds.

3.4. Movement of seasonal extreme isotherm locations

While the mean temperature at a location will be important for a species population, it is more likely to be extreme annual temperatures and the persistence of these extremes that

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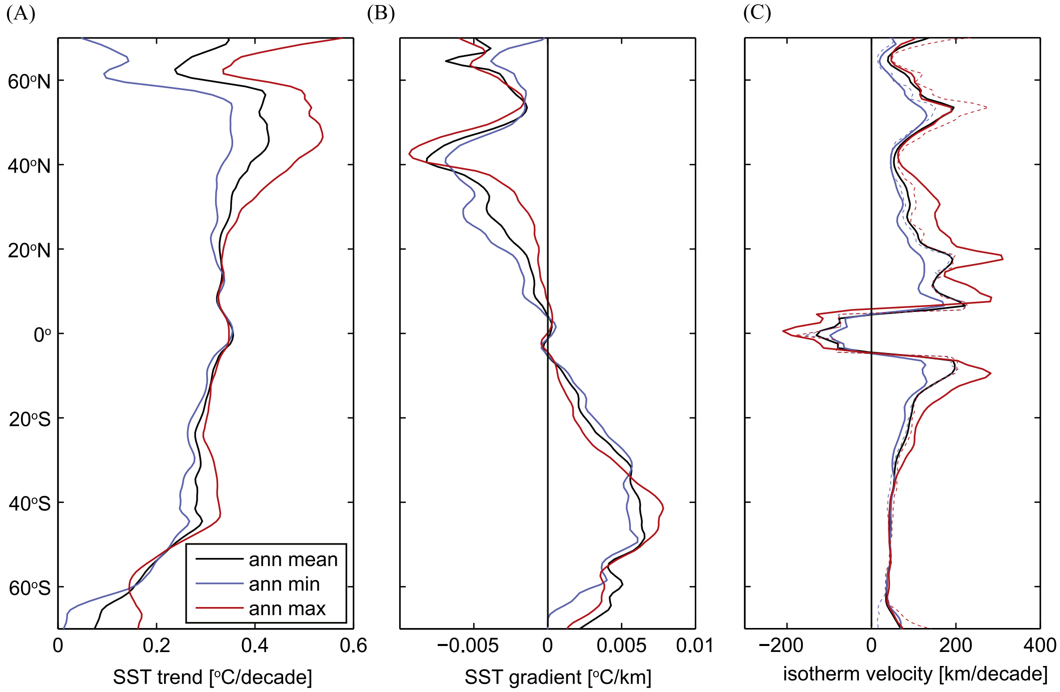

Fig. 4. Multi-model mean, zonally-averaged (median) (A) SST trend, for the 2006–2100 period, (B) meridional SST gradient and (C) poleward isotherm speed. Averages based on annual average (black), annual monthly maximum (red) and annual monthly minimum (blue) SST. Dashed lines indicate warm and cold season isotherm velocities calculated using the annual mean SST gradient. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

determine when and to where a population will migrate (as well as non-temperature related factors). Extreme high summer temperatures may cause stress, mortality and ultimately range contraction, while increased winter temperatures may allow for range expansion at the poleward limits of a population's distribution. For example, a recent extreme marine heat wave in Western Australia led to sustained temperatures up to 5 °C above normal for several weeks, leading to the localised extinction and range contraction of important habitat-forming algal species (Smale and Wernberg, 2013; Wernberg et al., 2013). The range expansion at the poleward limits of a population's distribution is exemplified by the increasing incursion of tropical species such as fishes and corals into temperate regions throughout the world (Baird et al., 2012; Feary et al., 2013; Yamano et al., 2011).

Fig. 3C–F shows SST trends and isotherm speeds for annual maximum and minimum temperatures. These are equivalent to maximum summer and minimum winter temperatures away from equatorial regions where there is very weak seasonality. While the patterns of warming share many similar features between hot and cold seasons, in most regions summer temperatures are projected to warm at a faster rate than winter temperatures in the ocean (Fig. 3C and E). This is clear when examining the zonally averaged SST trend (Fig. 4A), with the trends in annual maximum temperatures larger than the trends in annual minimum temperatures at most latitudes. This difference is largest in the northern hemisphere mid- and high-latitudes. This also implies that the seasonal range in SST will be considerably amplified in these regions according to the climate model projections. These enhanced summer SST trends contrast with the projected temperature changes over land, where winters are expected to warm faster than summers (Braganza et al., 2003) and could potentially lead to range contractions at the trailing edge of species distributions occurring at a faster rate than range expansions.

In the summer hemisphere meridional SST gradients tend to weaken at low latitudes (< 30–40° north and south), and tend to intensify at higher latitudes (Fig. 4B). Smaller meridional gradients in summer and to a lesser extent enhanced projected summer warming mean that isotherm movement is generally projected to be faster in the warm months at lower latitudes (away from the equator, where gradients are reversed; Fig. 4C). Projected isotherm speeds are also enhanced during summer at high latitudes in the northern hemisphere primarily due to the much larger warming trend in the warm season, discussed above. The effect of seasonal gradient and warming asymmetries tend to compensate at high southern latitudes resulting in little difference between projected summer and winter isotherm speeds. Overall the median 21st century isotherm speeds in the southern hemisphere are ~53 km/decade for the cold season and ~59 km/decade in the warm season. In the northern hemisphere the asymmetry is considerably greater; cold season speeds are ~77 km/decade and in the warm season are ~142 km/decade.

The calculation of isotherm speed provides an approximate estimate of the speed of an isotherm as it passes through a certain location; this speed will change with time and location. To examine the net shift in isotherms over time however, we can simply examine isotherm location at two times. Fig. 5 shows observed mean 1970–2010 location of selected warm and cold season isotherms and their projected positions at the end of the century. This is computed by adding the multi-model mean projected warm and cold season SST trends to the observed warm and cold season mean SST. Use of the observed SST as a starting point is a common method to reduce the effect of mean-state spatial biases in the models (although this approach cannot remove all model biases (Brown et al., this issue). We add a trend, rather than a difference to minimise the effect of aliasing by low frequency internal variability. It is apparent that based on RCP85 warming, the warm or cold boundaries of thermal habitats may move hundreds or in some cases thousands of kilometres polewards over the course of the next century. It is also apparent that certain cold temperature habitats will cease to exist, i.e. for certain high latitude populations whose thermal limits lie below these temperatures, there will be nowhere left to migrate. This is analogous to high-altitude species contracting to extinction in terrestrial systems, as suitable microclimates disappear from

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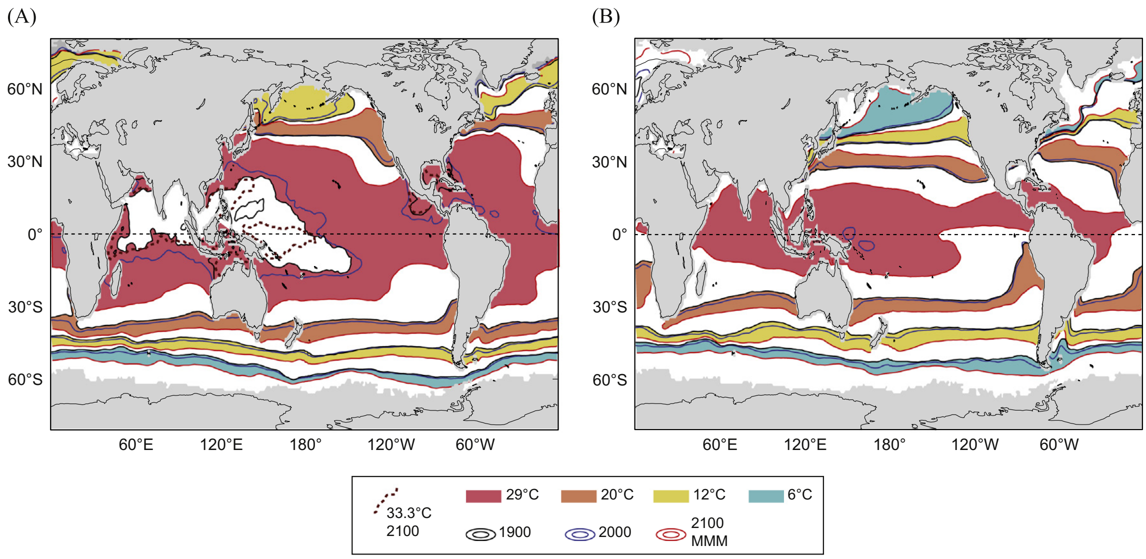

Fig. 5. Position of selected (6 °C, 12 °C, 20 °C, 29 °C and 33.3 °C) isotherms, based on (A) annual maximum SST and (B) annual minimum SST. Black, blue and red solid lines indicate isotherm locations in 1900, 2000 and 2100, respectively with coloured shading indicating the shift in isotherm location between 1900 and 2100. In order to minimise the effect of interannual variability the 1900 SST distribution is estimated as the 1970–2010 mean SST minus 90x linear SST annual trend averaged over the period 1900–2010 (i.e. $SST_{1970-2010}-90\times dSST/dt_{1900-2000}$), similarly the 2000 SST distribution is estimated as (i.e. $SST_{1970-2010}+10\times dSST/dt_{1900-2000}$). Projected isotherm locations are 'bias adjusted' i.e. calculated using mean observed (1970–2010) plus projected multi-model mean SST. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

mountaintops (Parmesan, 2006), and has very serious implications for numerous retreating species at the extreme northern and southern margins of continents (Wernberg et al., 2011).

At the warm extreme, new high temperature habitats will form at certain low latitude locations. For example, there are historically no marine regions where typical warm seasons temperatures exceed 33.3 °C (except for certain shallow coastal environments that are neither modelled by GCMs nor observed by satellites). However, extended regions of the western Pacific Warm Pool and tropical Indian Ocean are projected to exceed this temperature by the end of the century (under RCP85; Fig. 5B). Given that no populations currently have thermal limits that incorporate such high temperatures there may be a limited numbers of species that can populate these new high temperature habitats.

Particularly in tropical regions where north–south SST gradients are weak and there are strong east–west zonal SST gradients, pelagic populations may also migrate zonally to maintain their thermal preferences. In the tropical Pacific Ocean, for example, there is an almost 10 °C reduction in annual mean SST from the western Pacific Warm Pool to the eastern Pacific cold tongue region. As a result the location of the warm season 29 °C isotherm is projected to move from its historical location, close to the date line, to the eastern Pacific boundary over the course of the 21st century (Fig. 5B). This has important implications for Pacific skipjack tuna, the most important regional fishery (Bell et al., 2013), whose upper preferred temperature lies at approximately 29 °C. Of course, direct temperature effects are not the only factor that determines species ranges. Secondary effects of temperature on food availability, changes to species interactions and other criteria are also important aspects of where species can live and are often considered the most important proximate causes of climate-change related localised extinctions (Cahill et al., 2013). For Pacific skipjack tuna, however, projections suggest an eastward migration of tuna stocks away from the western Pacific as tropical SST warms using both temperature criteria alone (Ganachaud et al., 2012), as well as using a more sophisticated coupled physical-biogeochemical-tuna model (Bell et al., 2013; Lehodey et al., 2011). We note that while the 29 °C isotherm (which in the current climate is a useful proxy for the eastern edge of the Pacific Warm Pool) exhibits an enormous projected eastward shift, other dynamical features (e,g. the zonal convergence at the Warm Pool edge, which may be important for food accumulation) are unlikely to show such dramatic change (Brown et al., this issue).

3.5. Variability in the temporal evolution of isotherms

Ocean temperatures are subject to strong interannual variations and, as such, any poleward migration of species is unlikely to be gradual or monotonic. Indeed we demonstrated above that for decadal periods isotherms may exhibit strong equatorward shifts in some regions. In Fig. 6, we show examples of the latitudinal evolution of selected warm and cold season isotherms along three distinct coastlines: eastern Australia, northern Europe and California. We only show results from a single climate model, but similar behaviour is found in all the climate models.

For all isotherms shown there is a long-term poleward movement over the course of the 20th and 21st centuries. However, a number of additional characteristics can be identified. For many of the isotherms the interannual variability in latitude varies strongly over time. For example, the summertime location of the 26 °C isotherm along the east coast of Australia (Fig. 6A) has annual fluctuations of up to 500 km (i.e. ~5° of latitude) during the 20th century. This variability reduces considerably in the 21st century as the long-term mean isotherm location moves southwards. This behaviour is a result of spatial differences in the mean background meridional SST gradient. In regions of weak gradient a given change in SST, from one year to the next, will result in a larger isotherm displacement than in a region of strong meridional gradient. In the example described above, the mean 26 °C isotherm location lies in a region of very weak meridional SST gradient during the 20th century (Fig. 6A, side panel). The background SST gradient approximately doubles in magnitude as the isotherm migrates from ~30°S to ~32°S. Similar changes that are clearly linked to the background SST gradient are apparent for many isotherms in both northern Europe and California regions.

Another interesting characteristic is the lack of any long-term movement over extended periods of time followed by rapid displacements to a new latitudinal range. (Fig. 6). For example the

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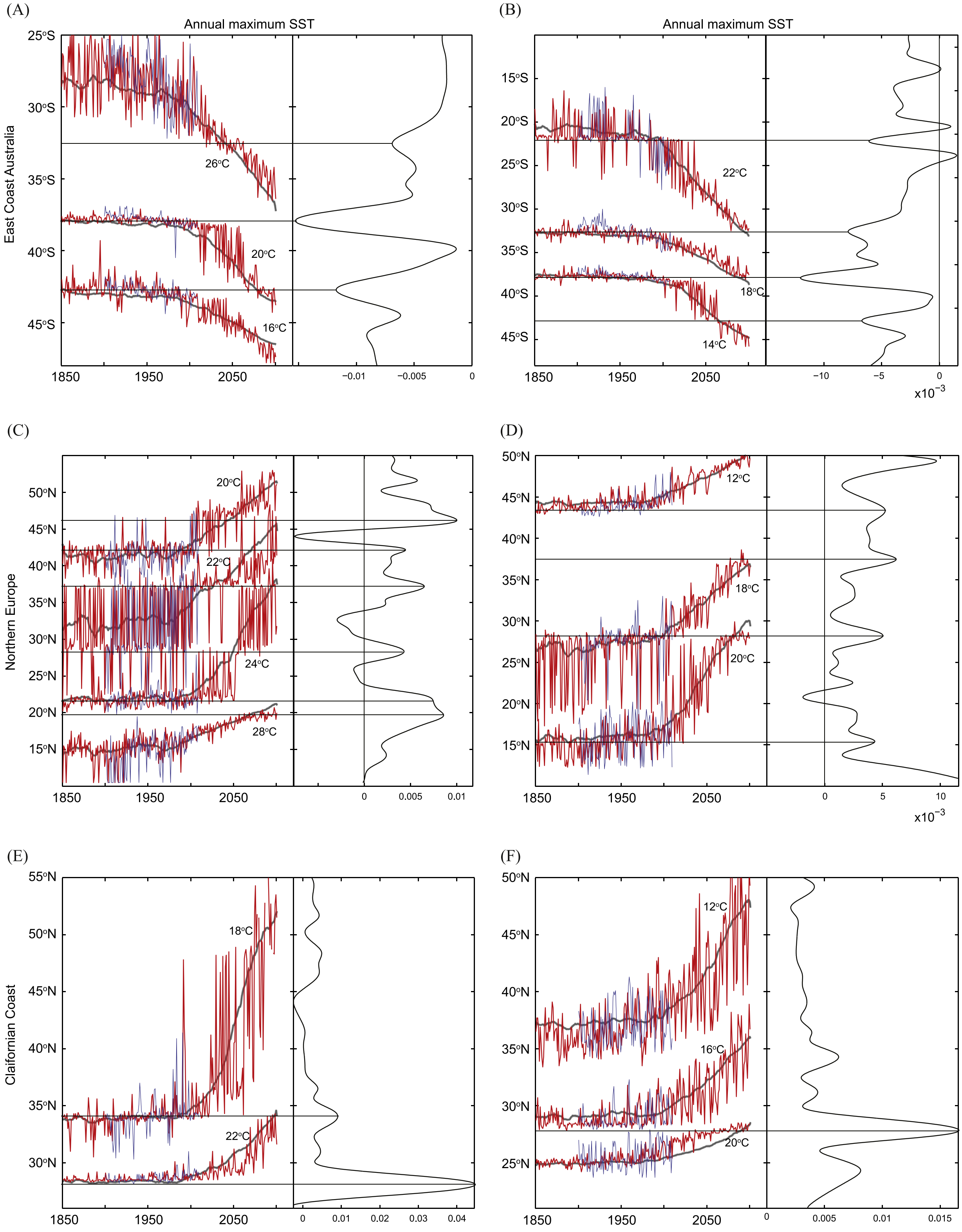

Fig. 6. Latitude of selected warm season (A, C, E) and cold season (B, D, F) isotherms along the coast of eastern Australia (a, B), Northern Europe (C, D) and the California Coast (E, F) for observations (blue), a single climate model (CCSM4, red; historical plus rcp85 scenario) and the multi-model mean (thick grey). Simulated SSTs have been bias corrected (i.e. the long term mean seasonal SST bias is removed from the model SST time series) prior to calculation of isotherm latitude. Side panels show the corresponding meridional SST gradient (units °C/km) with horizontal lines indicating the latitude of selected local peaks in the SST gradient. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

summertime latitude of the 24 °C isotherm adjacent to northern Europe (Fig. 6C) shows minimal long-term movement over the 20th century, an increase in interannual fluctuations between 2000 and 2050 and then a distinct shift to more poleward latitude range after ~2050, from where it never returns. The changes to the variability in the isotherms can be related back to the strength of the background SST gradient. Prior to 2000 the 24 °C isotherm undergoes only small latitudinal fluctuations close to 22°N, as it is situated in a region of relatively strong background meridional SST gradient (Fig. 6C, side panel). As noted above, where SST gradients are strong even large interannual changes in SST only lead to small isotherm displacements. Between ~2000 and 2050 the summertime isotherm latitude exhibits larger fluctuations along the coast of northern Europe between ~22°N and ~28°N, where another SST front exists. Finally, after ~2050 there is a very rapid transition to latitudinal fluctuations between 28°N and 37°N where a further SST front is found. During this period the 24 °C isotherm exhibits a variability range previously exhibited by the 22 °C isotherm during the 20th century as it is subject to the same background SST gradient. While interannual variability causes fluctuations in the latitude of a given isotherm, thermal fronts act as barriers that constrain these latitudinal variations. However as the background temperature increases, these barriers are ‘overrun’ and the isotherms can move rapidly across regions of relatively low meridional gradients until they encounter the next thermal front barrier. Again, this type of behaviour is apparent for different isotherms and regions. In summary, the background landscape in SST gradients is important for determining the size of interannual latitudinal variations in the location of isotherms. Moreover, the movement of isotherms in a warming world is often erratic, transitioning rapidly from one location to another, constrained by the location of thermal fronts.

This sporadic movement of isotherms is paralleled by observed changes in marine species ranges, which are also usually abrupt rather than gradual (Beaugrand et al., 2008; Harley and Paine, 2009; Smale and Wernberg, 2013). Moreover, the erratic and sudden movement of isotherms has important biological implications, as the lack of a gradual change in temperature may strongly limit the capacity of many species to adapt to a changing environment.

3.6. *Vertical movement of isotherms*

Finally, while we have primarily considered the poleward movement of thermal habitats as a result of long-term warming, some species may be able to adapt by moving deeper into the water column, taking advantage of the large vertical gradient in ocean temperature. Indeed, there exists some evidence of systematic depth increases across certain populations (e.g. Dulvy et al., 2008; Perry et al., 2005a). As an example of the potentially large vertical shift in thermally defined habitats, Fig. 7 shows the projected changes along the equator in the tropical Pacific. Following Ganachaud et al. (2012) we show isotherms related to the upper and lower thermal limits of skipjack tuna. Tuna tend to occur in water with temperatures between ~20 and ~29 °C, with thermal limits between about ~17 to ~30 °C (Bushnell and Brill, 1992). Fig. 7A shows the multi-model mean projected warming trend over the 21st century. As expected there is a surface intensified warming across the basin. Interestingly there is also a region of almost no warming situated at around 150 m close to the thermocline. This is thought to result from a dynamical raising of the thermocline (which causes a relative cooling along the thermocline, superimposed upon the surface intensified warming), as a result of a projected weakening of the equatorial Trade Winds (Han et al., 2006; Sen Gupta et al., 2012). Based on historical observations, there are no regions where annual mean temperatures exceed the tuna's upper limit of 30 °C. However, under future warming, the tropical Pacific reaches temperatures that exceed this limit everywhere west of ~140°W. Moreover, the temperature projections suggest that the tuna would have to go to depths of 50–100 m before reaching waters with temperatures lower than their thermal upper limit in the western and central Pacific.

As with the north–south movement of isotherms, shifts in isotherm depth also show strong internal variability and are also affected by vertical gradients in temperature. Fig. 7D, for example, shows the evolution of the depth of the 29 °C isotherm in the western equatorial Pacific, over the 21st century from the CCSM4 climate model (which has been shown to be one of the better performers in the western Pacific, (Brown et al., 2013). Over the first half of the century there are large vertical fluctuations in isotherm depth between the surface and ~100 m depth. In some months surface temperatures are less than 29 °C (indicated as missing values in Fig. 7d). The large fluctuations occur as the mixed layer temperature in the early part of the 21st century is also close to 29 °C, and so a small change in background temperature can cause a large vertical shift in isotherm depth. In the later half of the century the annual mean surface temperature exceeds 30 °C and the mean 29 °C isotherm depth now sits in the thermocline where the vertical gradient is much stronger than in the mixed layer. As such fluctuations in background temperature result in much smaller vertical isotherm movement, between ~80 and 120 m.

4. Discussion

Anthropogenic Global Warming can affect the ocean in a variety of ways (Brewer and Peltzer, 2009; Sen Gupta and McNeil, 2012). For example, there is already evidence for expansion of oxygen minimum zones, ocean acidification, modified circulation and nutrient supply, all changes that may affect marine habitats and are likely to be exacerbated in the future. Here, we focus on the role of a single but arguably the most important factor controlling marine habitats: changes in ocean temperature. We find that as the ocean warms, projected future shifts in thermal habitats that act to constrain marine species distributions are not a simple linear progression poleward. The movement of isotherms is erratic and depends on natural variability as well as long-term externally driven changes and is strongly affected by strength of temperature gradients and in particular the location of thermal fronts.

A number of studies have identified systematic changes in marine species, with poleward migrations towards cooler waters (e.g. Cheung et al., 2009; Drinkwater et al., 2010; Dulvy et al., 2008; Perry et al., 2005b; Sorte et al., 2010). However, care must be taken in linking migration with anthropogenic climate change, particularly when biological time series are relatively short (i.e. a few decades). Indeed in a recent review by Sorte et al. (2010) documenting range shifts in over 100 different marine species, covering a range of taxon, about 40% of studies where based on less than 20 years of observations. We have demonstrated that while we expect a poleward movement of thermal habitats over the long timescales over which anthropogenic climate change act, on decadal timescales SST fluctuations associated with low-frequency natural variability can dominate over anthropogenic warming. For example, we demonstrated that over two distinct 20-yr periods, the direction of isotherm movement implied by the observed temperature trends could change sign. In particular, isotherm speeds in many parts of the Pacific basin change direction depending on the state of the PDO. Indeed, many species have been shown to be sensitive to physical changes associated with the phase of the PDO (Richardson, 2008 and refereneces therein). In other locations, other natural climate fluctuations are likely to cause similar decadal or longer regional SST trends that may oppose or strengthen the anthropogenic-warming trend. For example, Oviatt (2004) documented the northward movement of various species in the North Atlantic, caused by rapid decadal warming periods (>2 °C/decade) in the 1930s and 1980s

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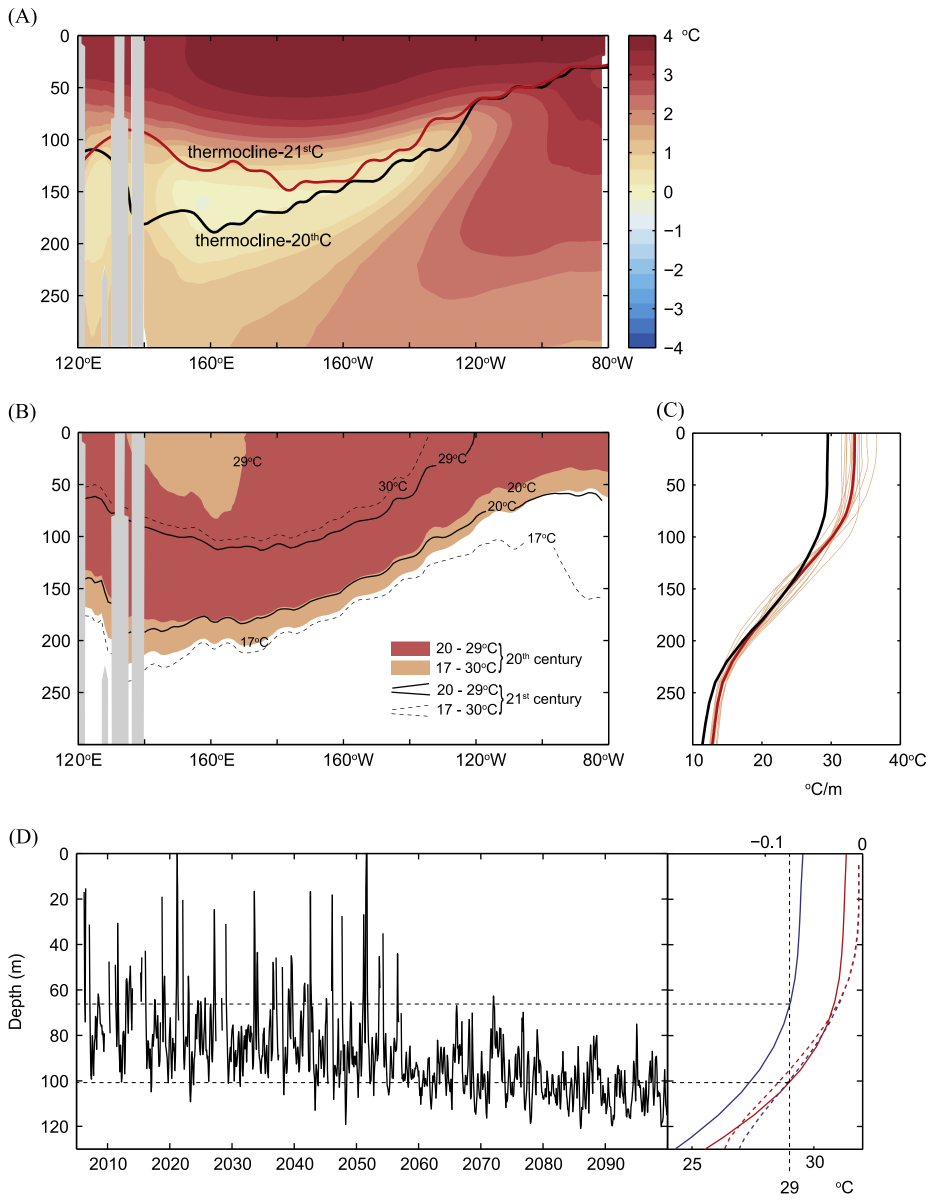

Fig. 7. Projected changes in subsurface temperature along the equatorial Pacific (3°S to 3°N). (A) Multi-model mean projected liner trend in potential temperature (~2005–2100, RCP85; shaded) with the location of the long-term mean observed 20th century (CARS2007: black line) and multi-model mean projected (observed + simulated trend: red line) thermoclines superimposed (calculated as the location of maximum vertical temperature gradient); (B) location of selected isotherms for the 20th century (observed) and 2100; (C) temperature profiles at 160°E for observed (black), projected individual models (thin red lines) and multi-model mean (thick red line); (D) monthly evolution of the 29 °C isotherm depth averaged between 170 and 180°E along the equator, side panel shows associated temperature with depth (solid lines) and temperature gradient with depth (dashed lines) averaged over the first 25 years (blue) and last 25 years (red) of the 21st century. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

associated with positive transitions of the North Atlantic Oscillation (NAO). Similarly, (Beaugrand et al., 2002) found that poleward shifts in copepod distributions over the latter half of the 20th century are related to both large-scale warming and NAO variability. Over longer timescales, SST changes of a few 10th of a degree over 20–40 yr are associated with the Atlantic Multidecadal Oscillation. In addition, external factors other than greenhouse gas changes, e.g. changes in ozone or aerosols can cause significant long-term regional cooling trends in SST.

As SST is an extensively observed property, we have a high confidence in our historical estimates of expected isotherm speeds. For example averaged over the 20th century we estimated median speeds of ~13 km/decade. A faster median speed of ~22 km/decade was estimated by Burrows et al. (2011), based on SST trends from 1960 to 2009, consistent with an acceleration of isotherm speeds with time. However, the expected speeds can be very different in different regions, largely because of differences in the background meridional SST gradient. In particular, we would expect faster speeds in regions of weak north–south SST gradients (for example in tropical regions away from the equator). A meta analysis of the literature by Sorte et al. (2010), indicated that 75% of the marine species examined had polewards range shifts (i.e in a direction consistent with anthropogenic warming) with an average rate of 19 km/year. However, this rate would be an order of magnitude faster than the median isotherm speeds during the 20th century and so not consistent with implied shifts in thermal habitats (although some of the discrepancy may be linked to changes in ocean circulation, e.g the acceleration of certain Western Boundary Currents Wu et al., 2012). Indeed, by using a more rigorous selection criteria of the studies included (e.g. by removing single-species studies, which tend to display a positive bias), Przeslawski et al. (2012) came up with a value an order of

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magnitude less than that estimated by Sorte et al. (2010) and consistent with the implied isotherm speeds presented here. Studies attempting to attribute species migration to anthropogenic climate change should carefully consider the regional SST changes over the associated time-period. Over certain regions and time periods shifts in thermal habitats may oppose or greatly amplify the long-term poleward trend.

To a large extent, isotherm speeds tend to scale with the rate of projected warming. As a result, based on the business-as-usual, RCP85 scenario migration speeds are projected to be 7–8 times faster than historically observed over the 20th century (based on the multi-model mean warming trend), with median speeds of about 80 km/decade. Again, this is subject to large regional variations.

A number of systematic features in projected warming are found across most climate models, which will influence the regional distribution of isotherm speeds. In particular, many western boundary current regions exhibit enhanced projected warming (consistent with changes that have already been observed, e.g. Wu et al., 2012) and the northern hemisphere mid-latitudes tend to warm faster than the southern hemisphere mid-latitudes in the future. The former has already led to particularly pronounced range shifts in the distribution of marine species in the northern hemisphere (Dulvy et al., 2008; Nye et al., 2009) and along many western boundary current regions such as off eastern North America (Fodrie et al., 2010; Parker and Dixon, 1998), Japan (Yamano et al., 2011) or eastern Australia (Last et al., 2011; Ling et al., 2009; Sorte, 2013). In addition, we find that in many regions summer temperatures warm faster than winter temperatures. This effect can be very significant (i.e. more than a two times difference), particularly in the northern hemisphere mid- and high-latitudes and implies a large amplification of the seasonal cycle. These enhanced summer SST trends are the opposite to what is projected (and what has already been observed) over land (Braganza et al., 2003). While this asymmetry has not been examined in detail here, we hypothesise that it may be related to the difference in mixed layer thickness between the seasons. As mixed layers are generally shallower in summer than in winter, an equal amount of heat uptake in both seasons would result in greater surface warming in summer.

Warmer summers would tend to be associated with range contraction (at the equatorward edge of a species thermal habitat) while warmer winters would tend to allow range expansion (at the poleward edge of a species thermal habitat). As such, in regions of large seasonal asymmetry in warming, we would expect an overall contraction in the area of thermal habitats.

By considering the interannual variability in extreme (summer and winter) isotherm locations, we have highlighted some important aspects of how migration progresses over time. Extreme isotherm latitudes are subject to sometimes-large interannual shifts. Over long time periods, as an isotherm migrates between regions with different background SST gradients, the size of the variability in the isotherms latitude can change dramatically, with greater variability associated with regions where the background SST gradient is weak. Moreover, we have demonstrated that oceanic fronts can act as barriers to the isotherm movement and therefore thermal habitat boundaries. Under a uniform rate of warming, isotherms will move slowly in regions of strong fronts and then rapidly across regions of low SST gradients. As such, rather than a gradual and monotonic poleward migration of thermal habitats we would expect (i) extended periods where habitat boundaries remain relatively stable in the vicinity of oceanic fronts (even when there is substantial warming), (ii) decadal or longer periods when the SST trend (associated with low frequency natural variability) would imply equatorward habitat movement or strongly amplified poleward movement, and (iii) rapid transitions in the location of a habitats from one thermal front to another.

In the same manner that terrestrial species can extend to higher altitudes to escape high temperatures, certain marine species may also be able to shift to greater depth where waters are cooler (Dulvy et al., 2008). Such shifts may have to be quite large, particularly in regions with deep isothermal mixed layers. For example, we showed that in the equatorial western Pacific the preferred thermal habitat for skipjack tuna moves eastward and deepens, consistent with previous results using CMIP3 (Ganachaud et al., 2012). Tuna would have to stay at depths of more than 50–100 m to be below their upper thermal maximum temperature, by the end of the century (under RCP85). Such changes would have important implications for catchability and so could adversely affect the fishery in the western Pacific. Moreover, the deepening of the preferred thermal habitat, in conjunction with a projected shoaling of the thermocline (which is tightly linked to the nutricline, primary productivity and the distribution of tuna forage) is likely to also affect tuna food availability.

Our study is subject to a number of limitations that should be considered. Both the observational record that we have employed and the climate models used for projections can only resolve temperatures at relatively low resolution (of the order of 100 km). As such, small-scale effects, which will be particularly important around high productivity coastal regions, are neglected (e.g. Karnauskas and Cohen, 2012). Indeed, by moving to higher resolutions that can explicitly resolve ocean eddies there is evidence that both the physical system (e.g. local SST) and biogeochemical systems may evolve quite differently compared to coarse resolution simulation (Matear et al., 2013). While we have generally focussed on the multi-model mean changes, different climate models exhibit a large range in projected warming rates (from about 2 °C to 4 °C/century under the RCP85 scenario, Fig. 3c). As a result there is approximately a factor of two uncertainty in isotherm speeds resulting from structural uncertainty in the models. Moreover, we have only considered a single future emissions pathway, the 'business as usual' RCP85 scenario. Lower emission scenarios will result in more moderate shifts in thermal habitats, which would scale approximately with the warming rates projected under these scenarios. While we have 'bias adjusted' projected results, removal of climate model errors with respect to the observed mean state is not without problems. Any errors in the simulation of variability are retained as are biases in projected trends that are associated with mean-state biases (e.g. Brown et al., this issue).

In summary, the movement of isotherms and associated thermal habitats that are an important factor in controlling species distributions are unlikely to be either uniform or monotonic. Low frequency variability on top of long-term anthropogenic warming implies that decadal scale migrations can be both poleward and equatorwards. Regional differences in north–south SST gradients means that isotherm speeds driven by anthropogenic warming are expected to be highly heterogeneous across different regions. Thermal fronts act as barriers to the poleward migration of isotherms. As such, in certain locations, the movement of thermal habitat boundaries will occur in sporadic jumps, with extended periods of little habitat movement followed by rapid transitions to new locations.

These results have important implications for studies aimed at attributing species shifts to anthropogenic warming. A poleward migration of a species by itself is not an indication of an anthropogenic cause. Careful consideration needs to be given to regional and temporal differences in thermal habitat movement.

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