

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

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2	warming ocean
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20	

#### 22 1 Abstract

23

24 Ocean temperatures have warmed in most regions over the last century and are 25 expected to warm at a faster rate in the future. Consistent with the view that marine 26 species are thermally constrained, there is growing evidence that many species have 27 already undergone poleward range shifts inline with warming trends. This study uses 28 historical observations of ocean temperature and climate model projections to 29 examine the implied migration of isotherms that mark the boundaries for species' 30 thermal habitats. In particular, we compare the rates of isotherm migration between 31 different ocean regions and at different time scales and examine to what extent the 32 implied migration is uniform or sporadic. Widespread long-term warming implies 33 poleward migration of isotherms in almost all regions. However, as the speed of 34 isotherm migration is inversely related to local meridional SST gradients and the 35 pattern of ocean warming is heterogeneous, migration speeds vary considerably 36 between regions, season and over time. On decadal timescales, changes due to low 37 frequency natural SST variability dominate over human induced changes. As such, 38 there are multi-decadal periods in certain regions when we would expect to see range 39 shifts that are much faster or in the opposite direction to that implied by 40 anthropogenic warming. Based on climate model projections, median isotherm 41 migration speeds will be about seven times faster in the 21<sup>st</sup> century compared to the 20th century under a business as usual emissions scenario. Moreover, SST warming is 42 43 projected to be greater in summer than in winter in most regions, contrary to what 44 happens over land. As such net isotherm migration speeds, particularly in the northern 45 hemisphere summer, are projected to be much faster than winter migrations. Finally 46 we show that isotherms may exhibit erratic migration rates over time, even under

uniform warming. Isotherms tend to remain co-located with a thermal front for
extended periods of time and then rapidly shift to a new position, marked by a more
poleward thermal front. This implies that species ranges would also be expected to
undergo sudden rapid shifts rather than exhibiting a gradual monotonic poleward
march.

52

#### 53 2 Introduction

54 All species or populations within a species have an optimal temperature range in 55 which they function most efficiently (Drinkwater et al., 2010; Huey and Kingsolver, 56 1989). Move too far outside a species' optimal range and its ability to function 57 degrades to a point where the population is no longer viable. Consequently, 58 temperature is often an important factor in determining the biogeography of a species. 59 This is particularly pertinent for marine species as they are typically more constrained 60 by thermal limits than terrestrial species (Sunday et al., 2012). Where there are long-61 term changes in the temperature of a region, for example driven by anthropogenic 62 climate change, a species population may be able tolerate the higher temperature, 63 although this may come at the cost of reduced efficiency (Drinkwater et al., 2010 and 64 references therein); the species population may move to a region with more 65 favourable temperatures, or the species population may become extinct. Even where a 66 species population can adapt to temperature changes, indirect effects may adversely 67 affect the population (e.g. Walther, 2010). New predator species may enter the region, 68 existing prey species may migrate away, the timing or phenology of predator prey 69 interactions may change or other physical or biogeochemical changes may occur (e.g. 70 changes in stratification, circulation or nutrient supply).

71

72 Over the last century, increased radiative forcing, driven primarily by rising concentrations of greenhouse gases, have resulted in a clear large-scale warming of 73 74 the earth surface including the upper ocean (Solomon et al., 2007). Given that 75 emissions of greenhouse gases are still accelerating (e.g. Raupach et al., 2007) further 76 warming, at faster rates, is expected. In conjunction with a large equator-to-pole 77 temperature difference, such broad scale warming will in most regions cause a 78 poleward migration of *thermally bound habitats*, the region between two isotherms 79 that border a species thermal range.

80

81 For terrestrial systems there is a large body of evidence for thermally driven species 82 migrations. For example Chen et al., (2011) performed a meta analysis of the 83 literature with regard to terrestrial range shifts. Based on a sample of over 700 species 84 from multiple taxa they found median polewards range shift speeds of  $\sim 17$ km/decade. 85 They also showed a significant correlation between the rate of range shift for species 86 and the associated rate of regional warming. Moreover, the correlation was increased 87 when this observed rate was compared with the theoretical rate of isotherm migration 88 speeds based on both the local rate of warming and regional differences in 89 temperature gradients (see below). While the evidence for marine species range shifts 90 is comparatively more limited, there is nevertheless compelling evidence of a 91 predominance of poleward range shifts (Nye et al., 2009; Perry et al., 2005a; 92 Przesławski et al., 2012; Wernberg et al., 2011). For example, a meta analysis by 93 Sorte et al., (2010) found a poleward migration in 75% of the (n=129) species 94 (including primary producers, fish, molluscs, crustaceans, birds, cnidarians and 95 sponges) for which there was evidence of a range shift. This is already having a

96 measurable impact on world fisheries, resulting in a global 'tropicalisation' of catch,

97 i.e. an increasing dominance of warm-water species (Cheung et al., 2013).

98

99 In this study we examine long-term observed surface isotherm migration speeds in 100 relation to spatial differences in meridional SST gradients (section 5.1) and contrast 101 this with speeds calculated on decadal timescales at which natural variability 102 dominates over anthropogenic changes (section 7.1). We then examine projections of 103 migration speeds based on the latest generation of climate models (section 10.1), for 104 the annual mean and for summer and winter seasons (section 10.2) and investigate 105 characteristics of the temporal evolution of isotherm locations subject to large 106 interannual variability and in regions of very different background spatial gradients 107 (section 10.3). Finally we briefly examine an alternative adaptation strategy available 108 to some species: vertical migration to greater depth (section 10.4). Implications for 109 marine species of these physical environmental changes and key recommendations are 110 provided in section Error! Reference source not found.

111

#### 112 **3 Methods**

113 Population distributions are set by a variety of physical and biogeochemical factors 114 including food availability, suitable habitat and predator and fishing pressures. One of 115 the primary abiotic constraints, however, is ocean temperature. Ocean temperature is a 116 well understood variable that has been routinely measured, particularly in the upper 117 ocean, over long periods of time. Moreover, climate models are able to simulate its 118 future evolution with a relatively high degree of confidence (Solomon et al., 2007) 119 compared to many other physical or biogeochemical characteristics of the ocean. Here 120 we examine observed and simulated surface and subsurface ocean temperature over 121 the historical period and projected temperature using the most recent generation of

122 coupled ocean-atmosphere climate models. We aim to provide insights into the

123 evolution of isotherms and by association thermally bound habitats in an ocean

subject to long term warming, strong interannual to multi-decadal variability and large

spatial heterogeneity.

126

The historical SST observations are based on the HadISST gridded dataset (Rayner et al., 2003). This provides spatially complete SST estimates at a 1°x1° resolution from 1871 to the present day, using in situ observations prior to 1981, and combining insitu 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 20<sup>th</sup> century are sparse (Deser et al., 2010).

134

135 Historical simulations and future projections of surface and subsurface temperature 136 are obtained from the state-of-the-art climate models taking part in the Coupled 137 Model Intercomparison Project phase 5 (CMIP5, Taylor et al., 2012). Historical 138 simulations are generally forced by observations of greenhouse gases, aerosols, ozone 139 and insolation, from approximately 1850 to 2005. To examine future changes, we use 140 simulations that follow the RCP85 emissions pathway (Riahi et al., 2007). This can be 141 considered as a 'business as usual' scenario in which greenhouse gas emissions remain large over the 21<sup>st</sup> century reaching ~1,370 CO<sub>2</sub>-equiv. in 2100 (Moss et al., 142 143 2010). The RCP85 scenario has been chosen here (rather than one of the lower 144 emissions pathways) as there is a large amount of model data available for this 145 scenario. It also offers the largest (climate change) signal to (internal variability) noise 146 ratio, making this scenario particularly useful for identifying robust climate change

147 patterns. We would expect similar results for lower emissions scenarios but with

148 correspondingly weaker projected warming and migration speeds. For SST

149 projections we use output from 27 different climate models, while for the subsurface

150 projections we use output from 17 models (see **Table 1**).

151

152 In the absence of other factors, we would expect range shifts of thermally sensitive species to be influenced by the migration of isotherms that mark species' thermal 153 154 limits. We follow the method of Loarie et al., (2009) and Burrows et al., (2011) to 155 estimate the temporally averaged north-south migration speeds of isotherms at a 156 certain location  $(\bar{v})$ . We calculate the ratio of the local temperature change 157 (calculated as a SST trend, from observations or climate models, over the desired 158 averaging period) to the local meridional SST gradient (calculated using SST 159 observations over a 1980-2010 reference period):

160

161 
$$\bar{v} = \overline{\left(\frac{\partial y}{\partial t}\right)} = \overline{\left(\frac{\partial SST}{\partial t}\right)} / \overline{\left(\frac{\partial SST}{\partial y}\right)}$$
 Equation 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 164 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.

169

### 170 4 The migration speed calculated with Equation 1 is an

### 171 approximation as both the instantaneous rate of change of SST

and the instantaneous SST gradient change with time. Differences 172 in SST trends and associated migration speeds over different time 173 periods are examined below. A sensitivity analysis demonstrates 174 that our results are relatively robust to the use of observed versus 175 176 simulated multi-model mean meridional SST gradients, as the multi-model mean gradients closely match the observed gradients 177 in most locations ( 178 179 Figure 1 a,b). Larger biases are evident for individual models. 180 181 Migration speeds and isotherm locations are calculated on annually averaged, annual 182 maximum and annual minimum temperatures (using monthly observational or climate 183 model data). Annual maximum or minimum temperatures generally correspond to 184 climatological maximum summer and minimum winter temperatures, except at low latitudes where the seasonal cycle is poorly defined. For the calculation of annual 185 186 maximum or minimum migration speeds we use meridional SST gradients calculated 187 from observed annual maximum or minimum temperatures, respectively. 188 5 **Results** 189

190 5.1 Historical long-term, isotherm migration speeds

191 6 Meridional gradients in mean SST show monotonically

decreasing temperatures from the equator to the poles for most

- 193 oceanic regions (
- Figure 1a). The most prominent exception to this is in the equatorial central andeastern 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 equatorial waters. Elsewhere, strong 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.

200

201	1 7 The speed with which isotherms at a certain location r	
202		poleward depends on both the local rate of change of SST and the

203 local meridional gradient in SST (Equation 1). Given the broad-

scale poleward gradient and the consistent centennial warming,

205 isotherms at almost all locations have, averaged over the last

### 206 **century, moved poleward (**

207 Figure 1d; the main exceptions being the parts of the tropical ocean where the local 208 SST increases towards the poles). However, large spatial differences are apparent. At 209 low latitudes, where SST gradients tend to be weak, speeds with which isotherms 210 move poleward tend to be larger. Interestingly, many of the regions of enhanced 211 warming, such as the Southern Ocean and the extensions of the Western Boundary 212 Currents, are not associated with particularly large speeds as meridional SST 213 gradients in these regions (i.e. the denominator in Eq. 1) are also large. Overall, all 214 ocean regions the median isotherm migration is ~13km/decade (Figure 2a; ~6 to 215 ~27km/decade interquartile range).

216

217 Climate models tend to under-predict the isotherm migration speed because they

218 underestimate the warming rate of the ocean. Based on the multi-model mean

estimate of historical warming from the climate models, simulated isotherm migration

220	spe	eds are in general weaker (median ~9km/decade). This is a results of a smaller
221	estimate of globally averaged SST warming in the climate models compared to the	
222	warming derived from HadISST (0.041°C/decade for the multi-model mean versus	
223	0.054°C/decade for HadISST, Figure 2c). The estimated migration speeds are	
224	rela	tively insensitive to whether we use the observed or multi-model mean meridional
225	SST	$\Gamma$ gradient (on the denominator of Equation 1) to calculate migration speeds
226	(Fig	gure 2a).
227		
228	7.1	Multi-decadal variability in isotherm migration
229	8	For most biological applications, decadal time scales are more
230		relevant than centennial ones. While some observational time-
231		series of marine populations cover centennial timescales
232		(generally associated with economically important species;
233		Cheung et al., 2009; Sorte et al., 2010), most biological time series
234		are much shorter. On the timescale of a few decades, natural
235		variability in SST will dominate over any long-term trend
236		associated with systematic increases in greenhouse gas
237		concentrations (e.g. Tebaldi and Knutti, 2007).
238	9	Figure 1 e and g show observed SST trends over two different 20-
239		years periods (1970-1990) and (1990-2010); the globally averaged
240		trends for these two periods are ~0.12°C/decade and
241		~0.07°C/decade, respectively, consistent with a faster rate of
242		global warming over recent decades (20 <sup>th</sup> century trend:

243	~0.054°C/decade). The trends are highly spatially heterogen	ieous
244	compared to the centennial scale trend (	
245	10 Figure 1c), with both warming and cooling trend magnitudes	
246	exceeding 0.6°C/decade in some regions. Moreover, across	
247	extended regions the trend changes direction between the t	WO
248	periods. For example, there is a strong warming in the cent	ral
249	and eastern tropical Pacific and northeastern Pacific, flank	ed by
250	cooling further west in the early period. This pattern rever	ses
251	sign in the later period. This ENSO-like SST pattern is	
252	characteristic of the low-frequency Pacific Decadal Oscillat	ion
253	(PDO; e.g. Mantua and Hare, 2002)/Interdecadal Pacific	
254	Oscillation (IPO; e.g. Power et al., 1999). Indeed, over the	970-
255	1990 period the PDO index was transitioning from a negati	ve to
256	positive state, while there was a negative transition between	n 1990
257	and 2010 (	
258	Figure 1i). Associated with the regional changes in SST trends are collocated	changes
259	in isotherm migration speeds. For example along the coast of California isoth	erms

migrated polewards, averaged over the 1970-1990 period but moved equatorwards
over the 1990-2010 period. Thus, we would expect a southward migration of certain
thermally sensitive species in this region over the most recent 20 years, opposite to
the direction that long-term warming 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

266 Koslow et al., 2013; Hsieh et al., 2009).

267

#### 268 10.1 Long-term Climate model projections

269 Over the 21<sup>st</sup> century the multi-model mean projected warming rate is ~7 times faster than for the 20<sup>th</sup> century under the RCP85 scenario (Figure 2c). Despite spatially 270 271 uniform increases in greenhouse gases, distinct regional differences in warming rate 272 become clear (Figure 3a). As noted for the historical trends, certain regions associated 273 with western boundary currents or their extensions exhibit enhanced warming. While 274 in other regions, such as the Southern Ocean, warming is relatively weak. This was 275 also found in for the CMIP3 models and is consistent with the projected 276 intensification of the surface westerlies and an associated increase in northward 277 Ekman transport of cold high latitude waters (Sen Gupta et al., 2009). There is also a 278 strong hemispheric asymmetry in warming particularly in the Pacific and Indian 279 basins, largely associated with differences in projected wind changes and associated 280 changes in evaporative ocean cooling. For example the projected intensification of the 281 south-easterly Trade Winds results in relatively weak warming in the south-eastern 282 Pacific, while the relatively strong warming along the equator and the northern Pacific 283 is associated with a weakening of the north-easterly and equatorial Trade Winds 284 (Timmermann et al., 2010; Xie et al., 2010).

285

Given the projected acceleration of warming across the oceans, projected poleward
migration speeds are correspondingly faster (Figure 2b, Figure 3b). Based on the
multi-model mean warming trend, median migration speeds for the 21<sup>st</sup> century are
~70km/decade (~42 to ~180km/decade inter quartile range) under RCP85, although
modal (most frequently simulated) speeds are considerably lower as a result of the

long tail of high migration speeds. Regional differences in migration speed are
generally similar, albeit considerably amplified, to those seen for the historical period
as these are largely determined by the spatial differences in meridional SST gradients.

294

A distinct northern-southern hemisphere asymmetry exists in the magnitude of

296 migration speeds. This is apparent for both historical and future isotherm speeds,

although much clearer for the projections. The median projected isotherm speed in the

southern hemisphere is  $\sim$ 57km/decade ( $\sim$ 41 to  $\sim$ 120km/decade inter quartile range)

compared to ~111km/decade (~55 to ~266km/decade) in the northern hemisphere,

300 under RCP85 (Figure 2b; positive/negative speeds are primarily from the

301 northern/southern hemisphere). This is partly due to the enhanced warming projected

302 in the northern hemisphere compared to the southern hemisphere: the hemisphere-

303 averaged warming is  $\sim 0.5$ C/100yr faster in the northern hemisphere (Figure 2c). More

304 important however is that meridional gradients generally tend to be weaker in the

305 northern hemisphere, leading to larger migration speeds.

306

307 The above results are based on the mean warming across 27 different climate models

308 (Table 1). It should be acknowledged, however, that there is a considerable spread in

309 the pattern and strength of warming across different models and associated migration

310 speeds. Rates of globally averaged SST warming over the 21<sup>st</sup> century, under RCP85,

311 range from ~2oC to ~4oC (Figure 2c). This corresponds to a range in median

312 migrations speeds across different climate models of ~38 to ~82km/decade in the

313 southern hemisphere and ~70 to ~156km/decade in the northern hemisphere (Figure

2b). That is, even if we had perfect knowledge of future CO2 concentrations we

would still have more than a factor of two uncertainty about isotherm migrationspeeds.

317

#### 318 **10.2** Migration of seasonal extreme isotherm locations

319 While the mean temperature at a location will be important for a species population, it 320 is more likely to be extreme annual temperatures that determine when and to where a 321 population will migrate (as well as non-temperature related factors). Extreme high 322 summer temperatures may cause stress, mortality and ultimately range contraction. 323 while increased winter temperatures may allow for range expansion at the poleward 324 limits of a population's distribution. For example, a recent extreme marine heat wave 325 in Western Australia led to sustained temperatures up to 5oC above normal for several 326 weeks, leading to the localised extinction and range contraction of important habitat-327 forming algal species (Smale and Wernberg, 2013; Wernberg et al., 2013). In 328 contrast, increased winter temperatures may allow for range expansion at the 329 poleward limits of a population's distribution; this is exemplified by the increasing 330 incursion of tropical species such as fishes and corals into temperate regions 331 throughout the world (Baird et al., 2012; Feary et al., 2013; Yamano et al., 2011). 332 333 Figure 3c-f shows SST trends and migration speeds for annual maximum and 334 minimum temperatures. These are equivalent to maximum summer and minimum 335 winter temperatures away from equatorial regions where there is very weak 336 seasonality. While the patterns of warming share many similar features between hot 337 and cold seasons, in most regions summer temperatures are projected to warm at a 338 faster rate than winter temperatures (Figure 3c and e). This is clear when examining 339 the zonally averaged SST trend (Figure 4a), with the trends in annual maximum

340 temperatures larger than the trends in annual minimum temperatures at most latitudes. 341 This difference is largest in the northern hemisphere mid- and high- latitudes. This 342 also implies that the seasonal range in SST will be considerably amplified in these 343 regions according to the climate model projections. These enhanced summer SST 344 trends contrast with the projected temperature changes over land, where winters are 345 expected to be warm faster than summers (Braganza et al., 2003) and could 346 potentially lead to range contractions at the trailing edge of species distributions 347 occurring at a faster rate than range expansions.

348

349 In the summer hemisphere meridional SST gradients tend to weaken at low latitudes 350 (<30-40° north and south), and tend to intensify at higher latitudes (Figure 4b). 351 Smaller meridional gradients in summer and to a lesser extent enhanced projected 352 summer warming mean that isotherm migration is generally projected to be faster in 353 the warm months at lower latitudes (away from the equator, where gradients are 354 reversed; Figure 4c). Projected migration speeds are also enhanced during summer at 355 high latitudes in the northern hemisphere primarily due to the much larger warming 356 trend in the warm season, discussed above. The effect of seasonal gradient and 357 warming asymmetries tend to compensate at high southern latitudes resulting in little 358 difference between projected summer and winter isotherm migration speeds. Overall 359 the median  $21^{st}$  century migration speeds in the southern hemisphere are ~53 360 km/decade for the cold season and ~59 km/decade in the warm season. In the northern 361 hemisphere the asymmetry is considerably greater; cold season speeds are  $\sim 77$ 362 km/decade and in the warm season are ~142km/decade. 363

364 The calculation of migration speed provides an approximate estimate of the speed of an isotherm as it passes through a certain location; this speed will change with 365 366 time/location. To examine the net effect of isotherm migration over time however, we 367 can simply examine the isotherm location at two times. Figure 5 shows observed 368 mean 1970-2010 location of selected warm and cold season isotherms and their 369 projected positions at the end of the century. This is computed by adding the multi-370 model mean projected warm and cold season SST trends to the observed warm and 371 cold season mean SST. Use of the observed SST as a starting point is a common 372 method to reduce the effect of mean-state spatial biases in the models (although this 373 approach cannot remove all model biases, (Brown et al., this issue)). We add a trend, 374 rather than a difference to minimise the effect of aliasing by low frequency internal 375 variability. It is apparent that based on RCP85 warming, the warm or cold boundaries 376 of thermal habitats may move hundreds or in some cases thousands of kilometres 377 polewards over the course of the next century. It is also apparent that certain cold 378 temperature habitats will cease to exist, i.e. for certain high latitude populations 379 whose thermal limits lie below these temperatures, there will be nowhere left to 380 migrate. This is analogous to high-altitude species contracting to extinction in 381 terrestrial systems, as suitable microclimates disappear from mountaintops (Parmesan, 382 2006), and has very serious implications for numerous retreating species at the 383 extreme northern and southern margins of continents (Wernberg et al., 2011). 384 385 At the warm extreme, new high temperature habitats will form at certain low latitude 386 locations. For example, there are historically no marine regions where typical warm

387 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; Figure 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.

394

395 Particularly in tropical regions where north-south SST gradients are weak and there 396 are strong east-west zonal SST gradients, pelagic populations may also migrate 397 zonally to maintain their thermal preferences. In the tropical Pacific Ocean, for 398 example, there is an almost 10°C reduction in annual mean SST from the western 399 Pacific Warm Pool to the eastern Pacific cold tongue region. As a result the location 400 of the warm season 29°C isotherm is projected to move from its historical location, 401 close to the date line, to the eastern Pacific boundary over the course of the 21st 402 century (Figure 5b). This has important implications for Pacific Skipjack Tuna, the 403 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 404 405 factor that determines species ranges. Secondary effects of temperature on food 406 availability, changes to species interactions and other criteria are also important 407 aspects of where species can live and are often considered the most important 408 proximate causes of climate-change related localised extinctions (Cahill et al., 2013). 409 For Pacific Skipjack Tuna, however, projections suggest an eastward migration of 410 tuna stocks away from the western Pacific as tropical SST warms using both 411 temperature criteria alone (Ganachaud et al., 2012), as well as using a more 412 sophisticated coupled physical-biogeochemical-tuna model (Bell et al., 2013; 413 Lehodey et al., 2011). We note that while the 29°C isotherm (which in the current

414 climate marks the boundary of the Pacific Warm Pool) exhibits an enormous

415 projected eastward shift other dynamical features (e,g. the zonal convergence at the

416 Warm Pool edge, which may be important for food accumulation) is unlikely to show

- 417 such dramatic change (Brown et al., this issue).
- 418

#### 419 **10.3 Sporadic Temporal Evolution of Isotherms**

420 Ocean temperatures are subject to strong interannual variations and, as such, any

421 poleward migration of species is unlikely to be gradual or monotonic. Indeed we

422 demonstrated above that for decadal periods isotherms may exhibit strong

423 equatorward migration in some regions. In Figure 6, we show examples of the

424 latitudinal evolution of selected warm and cold season isotherms along three distinct

425 coastlines: eastern Australia, northern Europe and California. We only show results

426 from a single climate model, but similar behaviour is found in all the climate models.

427

428 For all isotherms shown there is a long-term poleward migration over the course of the 20<sup>th</sup> and 21<sup>st</sup> centuries. However, a number of additional characteristics can be 429 430 identified. For many of the isotherms the interannual variability in latitude varies 431 strongly over time. For example, the summertime location of the 26°C isotherm along 432 the east coast of Australia (Figure 6a) has annual fluctuations of up to 500km (i.e.  $\sim 5^{\circ}$ 433 of latitude) during the 20<sup>th</sup> century. This variability reduces considerably in the 21<sup>st</sup> 434 century as the long-term mean isotherm location moves southwards. This behaviour is 435 a result of spatial differences in the mean background meridional SST gradient. In 436 regions of weak gradient a given change in SST, from one year to the next, will result 437 in a larger isotherm displacement than in a region of strong meridional gradient. In the 438 example described above, the mean 26°C isotherm location lies in a region of very

weak meridional SST gradient during the 20<sup>th</sup> century (Figure 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.

444

445 Another interesting characteristic is the lack of any long-term movement over 446 extended periods of time followed by rapid displacements to a new latitudinal range. 447 (Figure 6). For example the summertime latitude of the 24°C isotherm adjacent to 448 northern Europe (Figure 6c) shows minimal long-term movement over the 20<sup>th</sup> 449 century, an increase in interannual fluctuations between 2000-2050 and then a distinct 450 shift to more poleward latitude range after ~2050, from where it never returns. The 451 changes to the variability in the isotherms can be related back to the strength of the 452 background SST gradient. Prior to 2000 the 24oC isotherm undergoes only small 453 latitudinal fluctuations close to 22°N, as it is situated in a region of relatively strong 454 background meridional SST gradient (Figure 6c, side panel). As noted above, where 455 SST gradients are strong even large interannual changes in SST only lead to small 456 isotherm displacements. Between ~2000-2050 the summertime isotherm latitude 457 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 458 459 transition to latitudinal fluctuations between 28°N and 37°N where a further SST front 460 is found. During this period the 24°C isotherm exhibits a variability range previously exhibited by the 22°C isotherm during the 20<sup>th</sup> century as it is subject to the same 461 462 background SST gradient. While interannual variability causes fluctuations in the 463 latitude of a given isotherm, thermal fronts act as barriers that constrain these

464	latitudinal variations. However as the background temperature increases, these
465	barriers are 'overrun' and the isotherms can move rapidly across regions of relatively
466	low meridional gradients until they encounter the next thermal front barrier. Again,
467	this type of behaviour is apparent for different isotherms and regions. In summary, the
468	background landscape in SST gradients is important for determining the size of
469	interannual latitudinal variations in the location of isotherms. Moreover, the migration
470	of isotherms in a warming world is often erratic, transitioning rapidly from one
471	location to another, constrained by the location of thermal fronts.
472	
473	This sporadic movement of isotherms is paralleled by observed changes in marine
474	species ranges, which are also usually abrupt rather than gradual (Beaugrand et al.,
475	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 agradual change in temperature may strongly limit the capacity of many species to

- 478 adapt to a changing environment.
- 479
- 480

### 481 **10.4** Vertical migrations of isotherms

482 Finally, while we have primarily considered poleward migrations of thermal habitats 483 as a result of long-term warming., some species may be able to adapt by moving 484 deeper into the water column, taking advantage of the large vertical gradient in ocean 485 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 486 487 potentially large vertical shift in thermally defined habitats, Figure 7 shows the 488 projected changes along the equator in the tropical Pacific. Following Ganachaud et 489 al. (2012) we show isotherms related to the upper and lower thermal limits of skipjack 490 tuna. Tuna tend to occur in water with temperatures between 20 and 29°C, with

491 thermal limits between about 17 to 30°C (Bushnell and Brill, 1992). Figure 7a shows 492 the multi-model mean projected warming trend over the 21st century. As expected 493 there is a surface intensified warming across the basin. Interestingly there is also a 494 region of almost no warming situated at around 150m close to the thermocline. This is 495 thought to result from a dynamical raising of the thermocline (which causes a relative 496 cooling along the thermocline, superimposed upon the surface intensified warming), 497 as a result of a projected weakening of the equatorial Trade Winds (Han et al., 2006; 498 Sen Gupta et al., 2012). Based on historical observation, there are no regions where 499 annual mean temperatures exceed the tuna's upper limit of 30°C. However, under 500 future warming, the tropical Pacific reaches temperatures that exceed this limit 501 everywhere west of  $\sim 140^{\circ}$ W. Moreover, the temperature projections suggest that the 502 tuna would have to go to depths of 50-100m before reaching waters with temperatures 503 lower than their thermal upper limit in the western and central Pacific.

504

505 As with the north-south migration of isotherms, shifts in isotherm depth also show 506 strong internal variability and are also affected by vertical gradients in temperature. 507 Figure 7d, for example, shows the evolution of the depth of the 29°C isotherm in the 508 western equatorial Pacific, over the 21st century from the CCSM4 climate model 509 (which has been shown to be one of the better performers in the western 510 Pacific,(Brown and Langlais, submitted)). Over the first half of the century there are 511 large vertical fluctuations in isotherm depth between the surface and ~100m depth. In 512 some months surface temperatures are less than 29°C (indicated as missing values in 513 Figure 7d). The large fluctuations occur as the mixed layer temperature in the early 514 part of the 21st century is also close to 29°C, and so a small change in background 515 temperature can cause a large vertical shift in isotherm depth. In the later half of the

516 century the annual mean surface temperature exceeds 30°C and the mean 29°C

517 isotherm depth now sits in the thermocline where the vertical gradient is much

518 stronger than in the mixed layer. As such fluctuations in background temperature

result in much smaller vertical migrations of the isotherm, between ~80-120m.

520

#### 521 **11 Discussion**

522 The biogeography of marine populations is determined by a number of physical, 523 chemical and biological properties. Here, we focus on the role of changes in ocean 524 temperature as a driver of population relocation. We find that as the ocean warms, 525 projected future shifts in thermal habitats that act to constrain marine species 526 distributions are not a simple linear progression poleward. The movement of 527 isotherms is erratic and depends on natural variability as well as long-term externally 528 driven changes and is strongly affected by strength of temperature gradients and in 529 particular the location of thermal fronts.

530

531 A number of studies have identified systematic changes in marine species, with 532 poleward migrations towards cooler waters (e.g. Cheung et al., 2009; Drinkwater et 533 al., 2010; Dulvy et al., 2008; Perry et al., 2005b; Sorte et al., 2010). However, care 534 must be taken in linking migration with anthropogenic climate change, particularly 535 when biological time series are relatively short (i.e. a few decades). Indeed in a recent 536 review by Sorte et al., (2010) documenting range shifts in over 100 different marine 537 species, covering a range of taxon, about 40% of studies where based on less than 20 538 years of observations. We have demonstrated that while we expect a poleward 539 migration of thermal habitats over the long timescales over which anthropogenic 540 climate change act, on decadal timescales SST fluctuations associated with low-

541 frequency natural variability can dominate over anthropogenic warming. For example, 542 we demonstrated that over two distinct 20-yr periods, the direction of isotherm 543 migration implied by the observed temperature trends could change sign. In 544 particular, isotherm migrations in many parts of the Pacific basin change direction 545 depending on the state of the PDO. In other locations, other natural climate 546 fluctuations are likely to cause similar decadal or longer regional SST trends that may 547 oppose or strengthen the anthropogenic-warming trend. For example, Oviatt (2004) 548 documented the northward movement of various species in the North Atlantic, caused 549 by rapid decadal warming periods (>2°C/decade) in the 1930s and 1980s associated 550 with positive transitions of the North Atlantic Oscillation. Over longer timescales, SST changes of a few 10<sup>th</sup> of a degree over 20-40vrs are associated with the Atlantic 551 552 multi-decadal Oscillation (AMO; Ting et al., 2009). In addition, external factors other 553 than greenhouse gas changes, e.g. changes in ozone or aerosols can cause significant 554 long-term regional cooling trends in SST.

555

As SST is an extensively observed property, we have a high confidence in our 556 557 historical estimates of expected isotherm migration speeds. For example averaged over the 20th century we estimated median migrations speeds of ~13km/decade. A 558 559 faster median speed of ~22km/decade was estimated by Burrows et al., (2011), based 560 on SST trends from 1960-2009, indicating an acceleration of isotherm migration 561 speed with time. However, the expected migration speeds can be very different in 562 different regions, largely because of differences in the background meridional SST 563 gradient. In particular, we would expect faster migrations in regions of weak north-564 south SST gradients (for example in tropical regions away from the equator). A meta 565 analysis of the literature by Sorte et al., (2010), indicated that 75% of the marine

566	species examined had polewards range shifts (i.e in a direction consistent with
567	anthropogenic warming), with an average rate of 19km/year. However, this rate
568	would be an order of magnitude faster than the median migration speed of isotherms
569	during the 20 <sup>th</sup> century and so not consistent with implied shifts in thermal habitats.
570	Indeed, by using a more rigorous selection criteria of the studies included (e.g.
571	by removing single-species studies, which tend to display a positive bias),
572	Przesławski et al (2012) came up with a value an order of magnitude less than
573	that estimated by Sortes et al (2010) and consistent with the implied migration
574	speeds presented here. Studies attempting to attribute species migration to
575	anthropogenic climate change should carefully consider the regional SST changes
576	over the associated time-period. Over certain regions and time periods thermal habitat
577	migration may oppose or greatly amplify the long-term poleward trend.
578 579	In the future, migration speeds tend to scale with the rate of projected warming. As a
580	result, based on the business-as-usual, RCP85 scenario migration speeds could be 7-8
581	times faster than historically observed, with median migrations speeds of about
582	80km/decade. Again, this is subject to large regional variations.
583	
584	A number of systematic features in projected warming are found across most climate
585	models, which will influence the regional distribution of migration speeds. In
586	particular, many western boundary current regions exhibit enhanced projected
587	warming (consistent with changes that have already been observed, e.g. Wu et al.,
588	2012) and the northern hemisphere mid-latitudes tend to warm faster than the

southern hemisphere mid-latitudes in the future. This has already led to particularly

590 pronounced range shifts in the distribution of marine species in the northern

591 hemisphere (Dulvy et al., 2008; Nye et al., 2009) and along many western boundary 592 current regions such as Eastern North America (Fodrie et al., 2010; Parker and Dixon, 593 1998), Japan (Yamano et al., 2011) or Eastern Australia (Last et al., 2011; Ling et al., 594 2009; Sorte, 2013). In addition, we find that in many regions summer temperatures 595 warm faster than winter temperatures. This effect can be very significant (i.e. more 596 than a x2 difference), particularly in the northern hemisphere mid- and high-latitudes 597 and implies a large amplification of the seasonal cycle. These enhanced summer SST 598 trends are the opposite to what is projected (and what has already been observed) over 599 land (Braganza et al., 2003). While this asymmetry has not been examined in detail 600 here, we hypothesize that it may be related to the difference in mixed layer thickness 601 between the seasons. As mixed layers are generally shallower in summer than in 602 winter, an equal amount of heat uptake in both seasons would result in greater surface 603 warming in summer.

604

605 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

609 reduction in the area of thermal habitats.

610

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 can change dramatically, with

616 greater variability associated with regions where the background SST gradient is 617 weak. Moreover, we have shown that the existence of oceanic fronts act as barriers to 618 the migration of isotherms and therefore thermal habitat boundaries. Under a uniform 619 rate of warming, isotherms will migrate slowly in regions of strong fronts and then 620 rapidly across regions of low SST gradients. As such, rather than a gradual and 621 monotonic poleward migration of thermal habitats we would expect (i) extended 622 periods where habitat boundaries remain relatively stable in the vicinity of oceanic 623 fronts (even when there is substantial warming), (ii) decadal or longer periods when 624 the SST trend (associated with low frequency natural variability) would imply 625 equatorward habitat migrations or strongly amplified poleward migration, and (iii) 626 rapid transitions in the location of a habitats from one thermal front to another.

627

628 Just as terrestrial species can extend to higher altitudes to escape high temperatures, 629 certain marine species may also be able to shift to greater depth where waters are 630 cooler (Dulvy et al., 2008). Such shifts may have to be quite large, particularly in 631 regions with deep mixed layers. For example, we showed that in the equatorial 632 western Pacific the preferred thermal habitat for skipjack tuna moves eastward and 633 deepens, consistent with previous results using CMIP3 (Ganachaud et al., 2012). Tuna 634 would have to stay at depths of more than 50-100m to be below their upper thermal 635 maximum temperature, by the end of the century (under RCP85). Such changes would 636 have important implications for catchability and so could adversely affect the fishery 637 in the western Pacific. Moreover, the deepening of the preferred thermal habitat, in 638 conjunction with a projected shoaling of the thermocline (which is tightly linked to 639 the nutricline, primary productivity and the distribution of tuna forage) is likely to 640 also affect tuna food availability.

641

642 Our study is subject to a number of limitations that should be considered. Both the 643 observational record that we have employed and the climate models used for 644 projections can only resolve temperatures at relatively low resolution (of the order of 645 100km). As such, small-scale effects, which will be particularly important around 646 high productivity coastal regions, are neglected (e.g. Karnauskas and Cohen, 2012). 647 While we have generally focussed on the multi-model mean changes, different 648 climate models exhibit different projected rates of warming. As such there is a large 649 spread in possible projected isotherm migration speeds. Moreover, we have only 650 considered a single future emissions pathway, the 'business as usual' RCP85 scenario. 651 Lower emission scenarios will result in slower migration speeds, which would scale 652 approximately with the warming rates projected under these scenarios. While we have 653 'bias adjusted' projected results, removal of climate model errors with respect to the 654 observed mean state is not a fool proof method. Any errors in the simulation of 655 variability are retained as are biases in projected trends that are associated with mean-656 state biases (e.g. Brown et al., 2013, this issue).

657

In summary, migration of isotherms and associated the thermal habitats that are an

659 important factor in controlling species distributions are unlikely to be either uniform

or monotonic. Low frequency variability on top of long-term anthropogenic warming

661 implies that decadal scale migrations can be both poleward and equatorwards.

662 Regional differences in north-south SST gradients means that migration speeds driven

- by anthropogenic warming are expected to be highly heterogeneous across different
- regions. Thermal fronts act as barriers to poleward migration of isotherms. As such, in
- 665 certain locations, the movement of thermal habitat boundaries will occur in sporadic

jumps, with extended periods of little habitat movement followed by rapid transitionsto new locations.

668

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

673

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### 689 13 References

690	Anthony Koslow, J., Goericke, R., Watson, W., 2013. Fish assemblages in the
691	Southern California Current: relationships with climate, 1951–2008.
692	Fisheries Oceanography 22, 207–219.
693	Baird, A.H., Sommer, B., Madin, J.S., 2012. Pole-ward range expansion of Acropora
694	spp. along the east coast of Australia. Coral Reefs 31, 1063–1063.
695	Beaugrand, G., Edwards, M., Brander, K., Luczak, C., Ibanez, F., 2008. Causes and
696	projections of abrupt climate-driven ecosystem shifts in the North
697	Atlantic. Ecology Letters 11, 1157–1168.
698	Bell, J.D., Ganachaud, A., Gehrke, P.C., Griffiths, S.P., Hobday, A.J., Hoegh-Guldberg,
699	O., Johnson, J.E., Le Borgne, R., Lehodey, P., Lough, J.M., Matear, R.J.,
700	Pickering, T.D., Pratchett, M.S., Gupta, A.S., Senina, I., Waycott, M., 2013.
701	Mixed responses of tropical Pacific fisheries and aquaculture to climate
702	change. Nature Clim. Change advance online publication.
703	Braganza, K., Karoly, D., Hirst, A., Mann, M., Stott, P., Stouffer, R., Tett, S., 2003.
704	Simple indices of global climate variability and change: Part I – variability
705	and correlation structure. Climate Dynamics 20, 491–502.
706	Brown, J.N., Gupta, A.S., Brown, J.R., Muir, L.C., Risbey, J.S., Whetton, P., Zhang, X.,
707	Ganachaud, A., Murphy, B., Wijffels, S.E., 2013. Implications of CMIP3
708	model biases and uncertainties for climate projections in the western
709	tropical Pacific. Climatic Change 119, 147–161.
710	Brown, J.N., Langlais, C., submitted. Structure and Variability of Pacific Equatorial
711	SST and the edge of the Western Pacific Warm Pool in CMIP5. Climate
712	Dynamics.
713	Brown, J.N., Langlais, C., Sen Gupta, A., this issue. Projected temperature changes
714	to the equatorial Tropical Pacific adjusting for the cold tongue bias. Deep
715	Sea Research.
716	Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S.,
717	Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J.,
718	Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C.,
719	Schwing, F.B., Sydeman, W.J., Richardson, A.J., 2011. The Pace of Shifting
720	Climate in Marine and Terrestrial Ecosystems. Science 334, 652–655.
721	Bushnell, P.G., Brill, R.W., 1992. Oxygen transport and cardiovascular responses
722	in skipjack tuna (Katsuwonus pelamis) and yellowfin tuna (Thunnus
723	albacares) exposed to acute hypoxia. J. Comp. Physiol. B, Biochem. Syst.
724	Environ. Physiol. 162, 131–143.
725	Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J.,
726	Ryu, H.Y., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O., Wiens, J.J.,
727	2013. How does climate change cause extinction? Proc. R. Soc. B 280.
728	Chen, IC., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid Range
729	Shifts of Species Associated with High Levels of Climate Warming. Science
730	333, 1024–1026.
731	Cheung, W.W., Lam, V.W., Sarmiento, J.L., Kearney, K., Watson, R., Pauly, D., 2009.
732	Projecting global marine biodiversity impacts under climate change
733	scenarios. Fish and Fisheries 10, 235–251.
734	Cheung, W.W.L., Watson, R., Pauly, D., 2013. Signature of ocean warming in global
735	fisheries catch. Nature 497, 365–368.
736	Deser, C., Phillips, A.S., Alexander, M.A., 2010. Twentieth century tropical sea
737	surface temperature trends revisited. Geophys. Res. Lett. 37, L10701.

738	Drinkwater, K.F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R.I.,		
739	Pörtner, HO., Polovina, J.J., Takasuka, A., 2010. On the processes linking		
740	climate to ecosystem changes. Journal of Marine Systems 79, 374–388.		
741	Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmüller, V., Dye, S.R., Skjoldal, H.R.,		
742	2008. Climate change and deepening of the North Sea fish assemblage: a		
743	biotic indicator of warming seas. Journal of Applied Ecology 45, 1029–		
744	1039.		
745	Feary, D.A., Pratchett, M.S., J Emslie, M., Fowler, A.M., Figueira, W.F., Luiz, O.J.,		
746	Nakamura, Y., Booth, D.J., 2013. Latitudinal shifts in coral reef fishes: why		
747	some species do and others do not shift. Fish and Fisheries n/a-n/a.		
748	Fodrie, F.J., Heck, K.L., Powers, S.P., Graham, W.M., Robinson, K.L., 2010. Climate-		
749	related, decadal-scale assemblage changes of seagrass-associated fishes in		
750	the northern Gulf of Mexico. Global Change Biology 16, 48–59.		
751	Ganachaud, A., Sen Gupta, A., Brown, J., Evans, K., Maes, C., Muir, L., Graham, F.,		
752	2012. Projected changes in the tropical Pacific Ocean of importance to		
753	tuna fisheries. Climatic Change.		
754	Han, W., Meehl, G.A., Hu, A., 2006. Interpretation of tropical thermocline cooling		
755	in the Indian and Pacific oceans during recent decades. Geophys. Res. Lett		
756	33, 1961–2000.		
757	Harley, C.D., Paine, R.T., 2009. Contingencies and compounded rare		
758	perturbations dictate sudden distributional shifts during periods of		
759	gradual climate change. Proceedings of the National Academy of Sciences		
760	106, 11172–11176.		
761	Hsieh, CH., Kim, H.J., Watson, W., Di Lorenzo, E., Sugihara, G., 2009. Climate-		
762	driven changes in abundance and distribution of larvae of oceanic fishes		
763	in the southern California region. Global Change Biology 15, 2137–2152.		
764	Huey, R.B., Kingsolver, J.G., 1989. Evolution of thermal sensitivity of ectotherm		
765	performance. Trends in Ecology & Evolution 4, 131–135.		
766	Karnauskas, K.B., Cohen, A.L., 2012. Equatorial refuge amid tropical warming.		
767	Nature Climate Change 2, 530–534.		
768	Last, P.R., White, W.T., Gledhill, D.C., Hobday, A.J., Brown, R., Edgar, G.J., Pecl, G.,		
769	2011. Long-term shifts in abundance and distribution of a temperate fish		
770	fauna: a response to climate change and fishing practices. Global Ecology		
771	and Biogeography 20, 58–72.		
772	Lehodey, P., Hampton, J., Brill, R.W., Nicol, S., Senina, I., Calmettes, B., Pörtner,		
773	H.O., Bopp, L., Ilyina, T., Bell, J.D., others, 2011. Vulnerability of oceanic		
774	fisheries in the tropical Pacific to climate change. Vulnerability of Tropical		
775	Pacific Fisheries and Aquaculture to Climate Change'.(Eds JD Bell, JE		
776	Johnson and AJ Hobday.) pp 443–492.		
777	Ling, S.D., Johnson, C.R., Ridgway, K., Hobday, A.J., Haddon, M., 2009. Climate-		
778	driven range extension of a sea urchin: inferring future trends by analysis		
779	of recent population dynamics. Global Change Biology 15, 719–731.		
780	Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009.		
781	The velocity of climate change. Nature 462, 1052–1055.		
782	Mantua, N.J., Hare, S.R., 2002. The Pacific decadal oscillation. Journal of		
783	Oceanography 58, 35–44.		
784	Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren,		
785	D.P., Carter, T.R., Emori, S., Kainuma, M., Kram, T., Meehl, G.A., Mitchell,		
786	J.F.B., Nakicenovic, N., Riahi, K., Smith, S.J., Stouffer, R.J., Thomson, A.M.,		

787	Weyant, J.P., Wilbanks, T.J., 2010. The next generation of scenarios for
788	climate change research and assessment. Nature 463, 747–756.
789	Nye, J.A., Link, J.S., Hare, J.A., Overholtz, W.J., 2009. Changing spatial distribution
790	of fish stocks in relation to climate and population size on the Northeast
791	United States continental shelf. Marine Ecology Progress Series 393, 111–
792	129.
793	Oviatt, C.A., 2004. The Changing Ecology of Temperate Coastal Waters during a
794	Warming Trend. Estuaries 27, 895–904.
795	Parker, R.O., Dixon, R.L., 1998. Changes in a North Carolina Reef Fish Community
796	after 15 Years of Intense Fishing—Global Warming Implications.
797	Transactions of the American Fisheries Society 127, 908–920.
798	Parmesan, C., 2006. Ecological and evolutionary responses to recent climate
799	change, Annual Review of Ecology, Evolution, and Systematics 637–669.
800	Perry, A.L., Low, P.I., Ellis, I.R., Reynolds, I.D., 2005a, Climate Change and
801	Distribution Shifts in Marine Fishes. Science 308, 1912 –1915.
802	Perry, A.L., Low, P.L. Ellis, I.R., Reynolds, I.D., 2005b, Climate Change and
803	Distribution Shifts in Marine Fishes, Science 308, 1912–1915
804	Power S Casey T Folland C Colman A Mehta V 1999 Inter-decadal
805	modulation of the impact of FNSO on Australia Climate Dynamics 15
806	319–324
807	Przeslawski R Falkner I Ashcroft MR Hutchings P 2012 Using rigorous
808	selection criteria to investigate marine range shifts Estuarine Coastal and
800	Shelf Science 113, 205-212
810	Raunach M.R. Marland G. Ciais P. Quéré C.L. Canadell I.G. Klenner G. Field
811	C B 2007 Clobal and regional drivers of accelerating CO2 emissions
812	$PN\Delta S = 102.88 - 10293$
813	Rayner NA Parker DE Horton ER Folland CK Alevander I V Rowell DP
81 <i>1</i>	Kayner, N.A., Farker, D.L., Horton, E.D., Fonand, C.K., Alexander, E.V., Rowen, D.F.,
Q15	son ico, and night maring air temporature since the late ninoteenth
01J 816	contury I Coophys Dos 108 20 DD
817	Piabi K. Gr\üblar A. Nakiconovic N. 2007 Sconarios of long-tarm socio-
017	Rialli, K., Of (ublet, A., Nakicenovic, N., 2007. Scenarios of folig-term socio-
010 010	Technological Forecasting and Social Change 74, 997, 025
019	Son Cupto A Conschoud A McCrogor S Proum IN Muir I 2012 Drivers of
020	the projected changes to the Desific Ocean equatorial circulation
021	Coophys Dos Lott 20 100605
022	Geophys. Res. Lett. 59, L09005.
023	M.H. 2000. Drojected Changes to the Southern Hemionhers Ocean and Soc
024	M.H., 2009. Projected Changes to the Southern Hennsphere Ocean and Sea
020	Ice III the IPCC AR4 chillate Models. J. chillate 22, 5047–5076.
820	Smale, D.A., wernberg, 1., 2013. Extreme climatic event urives range contraction
827	Di a nabitat-forming species. Proceedings of the Royal Society B:
828	Biological Sciences 280.
829	Solomon, S., Qin, D., Manning, M., Alley, K.B., Berntsen, T., Bindoff, N.L., Chen, Z.,
830	Uniotnaisong, A., Gregory, J.M., Hegerl, G.C., 2007. Climate change 2007:
831	I ne physical science basis, contribution of working group 1 to the fourth
832	assessment report of the Intergovernmental Panel on Climate Change.
833	Sorte, C.J.B., 2013. Predicting persistence in a changing climate: flow direction
834	and limitations to redistribution. Oikos 122, 161–170.

835	Sorte, C.J.B., Williams, S.L., Carlton, J.T., 2010. Marine range shifts and species
836	introductions: comparative spread rates and community impacts. Global
837	Ecology and Biogeography 19, 303–316.
838	Sunday, J.M., Bates, A.E., Dulvy, N.K., 2012. Thermal tolerance and the global
839	redistribution of animals. Nature Clim. Change 2, 686–690.
840	Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An Overview of CMIP5 and the
841	Experiment Design. Bulletin of the American Meteorological Society 93,
842	485–498.
843	Tebaldi, C., Knutti, R., 2007. The use of the multi-model ensemble in probabilistic
844	climate projections. Philosophical Transactions of the Royal Society A:
845	Mathematical, Physical and Engineering Sciences 365, 2053–2075.
846	Timmermann, A., McGregor, S., Jin, F.F., 2010. Wind Effects on Past and Future
847	Regional Sea Level Trends in the Southern Indo-Pacific. Journal of Climate
848	23, 4429–4437.
849	Ting, M., Kushnir, Y., Seager, R., Li, C., 2009. Forced and internal twentieth-
850	century SST Trends in the North Atlantic*. Journal of Climate 22, 1469–
851	1481.
852	Walther, GR., 2010. Community and ecosystem responses to recent climate
853	change. Phil. Trans. R. Soc. B 365, 2019–2024.
854	Wernberg, T., Russell, B.D., Thomsen, M.S., Gurgel, C.F.D., Bradshaw, C.J.A.,
855	Poloczanska, E.S., Connell, S.D., 2011. Seaweed Communities in Retreat
856	from Ocean Warming. Current Biology 21, 1828–1832.
857	Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T.,
858	Bennett, S., Rousseaux, C.S., 2013. An extreme climatic event alters marine
859	ecosystem structure in a global biodiversity hotspot. Nature Clim. Change
860	3, 78–82.
861	Wu, L., Cai, W., Zhang, L., Nakamura, H., Timmermann, A., Joyce, T., McPhaden,
862	M.J., Alexander, M., Qiu, B., Visbeck, M., Chang, P., Giese, B., 2012.
863	Enhanced warming over the global subtropical western boundary
864	currents. Nature Climate Change 2, 161–166.
865	Xie, S.P., Deser, C., Vecchi, G.A., Ma, J., Teng, H., Wittenberg, A.T., 2010. Global
866	warming pattern formation: Sea surface temperature and rainfall. Journal
867	of Climate 23, 966–986.
868	Yamano, H., Sugihara, K., Nomura, K., 2011. Rapid poleward range expansion of
869	tropical reef corals in response to rising sea surface temperatures.
870	Geophysical Research Letters 38, n/a–n/a.
871	
072	

## 873 14 Tables

## **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-CHE	M 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

## 878 **15 Figures**

Figure 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 2100 period (where red/blue)

the associated isotherm migration speeds for the 1900 to 2100 period (where red/bluc 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)

- d) for the 1990 2010 (negative PDO transition) period. g) Smoothed PDO index
- 885 (http://jisao.washington.edu/pdo/PDO.latest). Colour bars are the same for panels 3, e
- 886 & g and for panels d, f & h.
- 887

888 Figure 2 a) Area weighted frequency distribution of north south isotherm speeds for 889 the historical period (1900-2010 HadISST: grey, 1900-2005 multi-model mean: 890 green) and projection for 2005-2100 (red). Shaded distributions are calculated using 891 the observed meridional SST gradient (dashed lines indicate associated distributions 892 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 893 894 distributions for individual models, thick black line is the multi-model mean and the 895 red and blue curves show two selected models with relatively high (red) and low 896 (blue) isotherm speeds. Closed circles above the curves indicate the median northward 897 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 898 899 models, respectively; vertical lines are the median northern and southern hemisphere 900 speeds (based on multi-model mean warming and the observed SST gradients). c) 901 Globally averaged rate of warming for individual models (1900-2005, historical 902 simulation: black circles; 2005-2100, rcp85 as red circles); black and red horizontal 903 lines are the associated multi-model mean warming trend and the green horizontal line 904 is the observed 1900-2005 trend; horizontal orange and blue lines indicate multi-905 model mean globally averaged trends based on annual maximum and minimum SST, 906 respectively.

907

Figure 3 a) Multi-model mean linear trend in SST based on RCP85 scenario; b)
average (2006-2100) projected meridional isotherm velocity calculated using equation
1. c & d (e & f) same as a & 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.

913

Figure 4 Multi-model mean, zonally averaged (median) a) SST trend, for the 20062100 period, b) meridional SST gradient and c) isotherm velocity. Averages

916 calculated based on annual average (black), annual monthly maximum (red) and

917 annual monthly minimum (blue) SST. Dashed lines indicate warm and cold season

- 918 isotherm velocities calculated using the annual mean SST gradient.
- 919

Figure 5 Position of selected isotherms (6°C, 12°C, 20°C, 29°C and 33.3°C) in 1900,
2000 and 2100 based on a) annual minimum SST and b) annual maximum SST.
1900 (2000) SST has been calculated as 1970-2010 mean SST minus (plus) 90 (10) x
linear SST trend [per annum] calculated over 1900-2010 period, in order minimise the
effect of interannual variability. Projected isotherm locations are 'bias adjusted' i.e.
calculated using mean observed (1970-2010) plus projected multi-model mean SST.

- 927 Figure 6 Latitude of selected warm season (a,c,d) and cold season (b,d,f) isotherms
- along the coast of eastern Australia (a,b), Northern Europe (c,d) and the California
- 929 Coast (e,f) for observations (blue), a single climate model (CCSM4, red; historical
- 930 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
- 933 corresponding meridional SST gradient (units °C/km)
- 934
- 935 Figure 7 Projected changes in subsurface temperature along the equator (3°S to 3°N).
- a) Multi-model mean projected liner trend in potential temperature (~2005-2100,
- 937 RCP85; shaded) with the location of the long-term mean observed 20<sup>th</sup> century
- 938 (CARS2007: black line) and multi-model mean projected (observed + simulated
- trend: red line) thermoclines superimposed (calculated as the location of maximum
- 940 vertical temperature gradient); b) location of selected isotherms for the 20<sup>th</sup> century
- 941 (observed) and 2100; c) temperature profiles at 160°E for observed (black), projected
- 942 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  $21^{st}$  century.
- 947
- 948
- 949

## 1 1 Figures



- 3 Figure 1 Warming trend (a, c & e) and poleward isotherm speed (c, d & f) for 1900 to
- 4 2100 (a & b), 1970 1990 (c & d, PDO positive transition period) and 1990 2010 (e
- 5 & f, PDO negative transition period). g) Smoothed PDO index
- 6 (http://jisao.washington.edu/pdo/PDO.latest). Shading indicated region of low
- 7 meridional SST gradient (< 1oC/1000km). NB Red (blue colours) on left panels
- 8 indicate poleward (equatorward) isotherm migration speeds.
- 9 [plot\_HadISST\_maps\_PDO.m]
- 10 11
- 11



Figure 2 Meridional SST gradient based on a) HadiSST and b) multi-model mean; c) Multi-model mean linear trend in SST based on RCP85 scenario (mottling indicates 14

- regions where at least 75% of models agree that the warming will be faster or slower 15
- than the global mean); d) Average (2006-2100) projected meridional isotherm 16
- 17 velocity calculated as dSST/dt/dSST/dy. e & f (g &h) same as c & d but using annual
- 18 minimum (maximum) SST.
- 19 [plot\_projection\_map\_figure.m]
- 20
- 21



isotherm velocity [km/decade]
SST gradient [°C/km]
SST trend [°C/decade]
Figure 3 Multi-model mean, zonally averaged (median) a) isotherm velocity, b)
meridional SST gradient and c) SST trend, for the 2006-2100 period. Averages
calculated 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.

- 28 [plot\_projection\_map\_figure.m]
- 29
- 30
- 31
- 32



33 34 Figure 4 a) area weighted frequency distribution of north south isotherm velocity for 35 the historical period (1900-2010 HadISST: black, 1900-2005 multi-model mean: green) and projection for 2005-2100 (red). Distributions are calculated using the 36 37 observed/multi-model mean meridional SST gradient (shaded/dashed lines). Area 38 under the distributions are defined to be equal to 1. Solid lines show the cumulative 39 frequency distributions associated with the shaded distributions. b) as a) but for 40 projected distributions only. Grey lines represent distributions for individual models, 41 black line is the multi-model mean and the red and blue curves show two selected 42 models with relatively high (red) and low (blue) velocities. Black points above the 43 curves indicate the median of the northward and southward velocities; vertical line is 44 median for the multi-model mean; red and blue circles are median for the high and 45 low velocity models. c) globally averaged rate of warming for individual models 46 (1900-2005, historical simulation: clack points; 2005-2100, rcp85: red points); black 47 and red horizontal lines are the associated multi-model mean warming trend and the 48 green horizontal line is the observed 1900-2005 trend. Dashed horizontal lines 49 indicate multi-model mean globally averaged trends at each location of annual 50 maximum (red) and minimum (minimum) SST. As (b) projected distributions of 51 annual mean (black, same as curve shove in panel b), annual maximum (red) and 52 annual minimum (blue) trends. Vertical lines indicate the associated median 53 northward and southward velocities. [plot PDF figure.m] 54

55



58 Figure 5 Position of selected isotherms (6°C, 12°C, 20°C and 29°C) in 1900, 2000 and

- 59 2100. 1900 (2000) SST based on a) annual minimum SST and b) annual maximum
- 60 SST. Calculated as 1970-2010 mean SST minus (plus) 90 (10) x linear SST trend [per
- annum] calculated over 1900-2010 period; this minimises the effect of interannual
- 62 variability. Projected isotherm locations calculated using mean observed (1970-2010)
- 63 plus projected multi-model mean SST. [plot\_isotherm\_minmax.m]



Figure 6 Latitude of selected warm season (a,c,d) 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 SST have been bias corrected (i.e. the long term mean seasonal SST bias is removed from the model SST timeseries) prior to calculation of isotherm latitude. Side panels show the corresponding meridional SST gradient (units <sup>o</sup>C/km)



<sup>72</sup> <sup>120°E</sup> <sup>160°E</sup> <sup>160°W</sup> <sup>120°W</sup> <sup>80°W</sup> <sup>10</sup> <sup>20</sup> <sup>30</sup> <sup>40°</sup>
<sup>73</sup> Figure 7 Projected changes in thermal properties along the equator (3oS to 3oN). a)
<sup>74</sup> multi-model mean projected liner trend in potential temperature (~2005-2100,
<sup>75</sup> RCP85; shaded) with the location of the long-term mean observed 20<sup>th</sup> century
<sup>76</sup> (CARS2007: black line) and multi-model mean projected (observed + simulated
<sup>77</sup> trend: red line) thermoclines superimposed (calculated as the location of maximum

78 vertical temperature gradient); b) location of selected isotherms for the 20<sup>th</sup> century

79 (observed) and 2100, relevant to skipjack tuna; c) temperature profiles at 1600E for

80 observed (black), projected individual models (thin red lines) and multi-model mean

- 81 (thick red line).
- 82