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Climate change is projected to reduce carrying capacity and redistribute species richness in North Pacific pelagic marine ecosystems

Running head: Climate change may reduce carrying capacity

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Abstract

Climate change is expected to impact all aspects of marine ecosystems, including fisheries. Here, we use output from a suite of 11 earth system models to examine projected changes in two ecosystem-defining variables: temperature and food availability. In particular, we examine projected changes in epipelagic temperature and, as a proxy for food availability, zooplankton density. We find that under RCP8.5, a high business-as-usual greenhouse gas scenario, increasing temperatures may alter the spatial distribution of tuna and billfish species richness across the North Pacific basin. Furthermore, warmer waters and declining zooplankton densities may act together to lower carrying capacity for commercially valuable fish by 2 – 5% per decade over the 21st century. These changes have the potential to significantly impact the magnitude, composition, and distribution of commercial fish catch across the pelagic North Pacific. Such changes will in turn ultimately impact commercial fisheries' economic value. Fishery managers should anticipate these climate impacts in order to ensure sustainable fishery yields and livelihoods.

Introduction

Pelagic marine habitat is projected to experience a number of impacts from climate change (*e.g.*, Bopp *et al.*, 2013). As earth system models improve with each model generation, confidence in their projections has increased and a community consensus is coalescing around several projected impacts. Of these, two of the most significant impacts to epipelagic habitat are likely to be ocean warming (Bopp *et al.*, 2013) and the expansion of the oligotrophic subtropical gyres (Sarmiento *et al.*, 2004; Steinacher *et al.*, 2010; Polovina *et al.*, 2011; Cabré *et al.*, 2015). Ocean warming is a direct result of ocean heat uptake in response to atmospheric warming driven by increasing greenhouse gas concentrations. Gyre expansion is projected as the result of two physical mechanisms. Ocean heating leading to increased vertical stratification is expected to further reduce nutrient concentrations in the euphotic zone of oligotrophic gyre waters (Xu *et al.*, 2012; Cabré *et al.*, 2015). Additionally, changes in atmospheric circulation may result in a poleward displacement of both the descending branch of the Hadley circulation and of mid-latitude storm tracks (Chang *et al.*, 2012; Scheff *et al.*, 2012; Yongyun *et al.*, 2012; Cabré *et al.*, 2015). These changes in atmospheric circulation will in turn alter ocean surface wind stress curl, primarily along the gyres' poleward boundaries, contributing to gyre expansion.

Change in the biophysical marine environment will impact many marine organisms, as well as fisheries and those who rely on fishery services. Catch from pelagic fisheries in the North Pacific is largely comprised of tuna, including skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), and bigeye (*Thunnus obesus*), as well as other species (FAO, 2012). Tunas occupy specific thermal habitats at different life stages and have a high metabolic demand (Lehodey *et al*., 2011, 2013). Thus, changes to either thermal habitat or ocean productivity are likely to impact tunas, as well as other commercially valuable fish. We examine these climate change impacts through a suite of models included in the fifth phase of the Coupled Model Intercomparison Project (CMIP5; Taylor *et al*., 2012), focusing on the two habitat parameters that most directly influence ecosystem productivity and capacity: temperature and food availability. We aim to make broad projections of climate change impacts on marine fisheries that can be used by fishery managers when drafting ecosystem-based fisheries management plans. Previous studies have suggested that climate change may have a substantial impact on commercial fish catch, independent of fishing (Cheung *et al*., 2010; Lehodey *et al*., 2011, 2013; Bell *et al*., 2013; Howell *et al*., 2013; Woodworth-Jefcoats *et al*., 2015). Therefore, it is essential that these potential impacts be incorporated into management plans so that both fishery resources and livelihoods can be sustained well into the future.

Materials and methods

Earth system models used

We examine 11 earth system models included in CMIP5. Models used are presented in Table 1. Models selected are those with two trophic levels (phyto- and zooplankton) of output available at time of download. All data were downloaded from the CMIP5 data portal (http://cmip-pcmdi.llnl.gov/cmip5/data_portal.html). Spherical interpolation (for curvilinear grids) and nearest coordinate regridding (for rectilinear grids) were used to regrid output to a common 1° × 1° rectilinear grid spanning 0 – 66°N and 120°E – 70°W, with the Bering Sea and Sea of Okhotsk excluded. We note that output from two additional models, HadGEM2-CC and

HadGEM2-ES (Collins *et al*., 2011), was available but not used in our analysis due to unrealistic negative plankton densities across much of the central North Pacific.

Data used

Both historical and projected data are examined. All projections are from the representative concentration pathway (RCP) 8.5 scenario, "a relatively conservative business as usual case… with no explicit climate policy" (Riahi *et al*., 2011). We focus on two 20-year time periods representing the beginning and end of the 21st century: 1986 – 2005 and 2081 – 2100. The beginning of the 21st century is captured by the last 20 years of the historical runs and the end of the 21st century by the last 20 years of the 21st century in the RCP8.5 projection.

Data are vertically integrated across the epipelagic zone, represented as the upper 200 m of the water column. Vertical resolution varies by model and we integrated across all depths of 200 m or less. We examine potential temperature, phytoplankton carbon density, and zooplankton carbon density output by each model. Data are examined as a model ensemble to address the possible influence of individual model drift (Sen Gupta *et al*., 2013).

Vertically integrated (upper 200 m) ocean temperatures from the World Ocean Atlas 2013 (WOA13; Locarnini *et al*., 2013) were used as baseline temperatures when calculating projected ecosystem impacts (see below). The temperature increase projected by each model was then added to the WOA13 data to determine projected ecosystem change.

Pelagic habitat

We examine changes in thermal habitat by comparing probability frequency distributions of pooled 20-year, monthly epipelagic temperatures. Because so much of the literature is focused on SST, we also present projected changes in SST though these changes are not the focus of our analysis. In both cases, monthly temperatures were used in an effort to fully capture seasonal extremes and distributions are binned in 0.5 °C bins. Change in zooplankton densities are similarly compared, though annual densities are used as this is the only temporal scale available for three-dimensional biogeochemical data through the CMIP5 data portal. Distributions are binned in 0.05 g C m^{-2} bins. Twenty-year means from the beginning and end of the 21st century (see above) are used to evaluate the absolute change in epipelagic temperature and percent change in both phyto- and zooplankton densities.

Ecosystem impacts

We assess two measures of ecosystem impact: tuna and billfish species richness and carrying capacity. Species richness captures the total number of tuna and billfish species present and carrying capacity the total number of fish the ecosystem can support. Species richness (SR) is a function of epipelagic temperature, following equation 1 as determined by Boyce *et al*. (2008),

$$SR = -0.0033T^{3} + 0.1156T^{2} - 0.4675T \qquad (1)$$

where T is epipelagic temperature in °C. Carrying capacity (K) is determined from ecological theory, following equation 2,

$$K \propto [R] M^{-3/4} e^{E/kT} \qquad (2)$$

where $[R]$ is limiting resource supply, which we take as zooplankton density, M is target fish mass, E is activation energy (0.63 eV; Brown *et al*., 2004), k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}; Brown *et al*., 2004; Jenning *et al*., 2008), and T is epipelagic temperature in Kelvin (Brown *et al*., 2004). Given that Eq. 2 is a proportional relationship, we evaluate relative changes in the right-hand-side of the equation and refer to these as changes in potential carrying capacity (K_p). Twenty-year means from the beginning and end of the 21st century are used to evaluate changes in SR and K_p. We hold M constant over both periods so the resulting change in K_p is independent of M. To assess whether R or T has a greater influence on K_p we examine the difference between the absolute percent change in both R and $e^{E/kT}$ following equation 3,

$$|\%\Delta R| - |\%\Delta e^{E/kT}| \qquad (3)$$

with positive results indicating that changes in zooplankton density have the greatest influence on K_p and negative results indicating that changes in T have the greatest influence on K_p.

Results

Pelagic habitat

Thermal habitat

Across all models, sea surface and epipelagic temperatures are projected to increase (Table 1, Figs. 1a and 2a). Additionally, all model scenarios project the emergence of new, warmer temperatures by the end of the 21st century. Emerging SSTs (*i.e.*, temperatures not present at the beginning of the 21st century that are present at the end of the 21st century) range from 31.5 – 38 °C and epipelagic temperatures from 29 – 35 °C. Change in thermal habitat is also captured through the difference between frequency distributions over time. Epipelagic temperatures that comprise the majority of the North Pacific at the beginning of the 21st century (15.6 – 23.7 °C on average) decline in frequency and warmer temperatures come to dominate by the end of the century (24.5 – 32.9 °C on average).

Our results focus on the warmest temperatures in the North Pacific as these temperatures cover the largest area. However, it is important to note that there is a similar distributional shift in the coolest temperatures. Here, too, there is model consensus on a shift towards warmer temperatures, as well as a loss of the coolest temperatures by the end of the 21st century (Fig. 1a). Across all models, disappearing epipelagic temperatures range from -1.5 – 2 °C. Three models (IPSL-CM5B-LR, MPI-ESM-LR, and MPI-ESM-MR) project a loss of the coolest SSTs, ranging from -2.0 – -1.0 °C.

Food available to fish

We take zooplankton density to be a proxy for food available to fish. Across all models, the distribution of zooplankton densities is projected to shift towards lower values (Table 1, Figs. 1b and 2b). Densities that comprise the majority of the North Pacific at the beginning of the 21st century (0.50 – 1.10 g C m^{-2} on average) decline in frequency and lower densities come to dominate by the end of the century (0.18 – 0.49 g C m^{-2} on average).

Not only do the models used in our study project zooplankton densities to decline across much of the North Pacific, but they also project these declines to be amplified relative to declines in phytoplankton densities (Fig. 2c, warm colors represent waters where zooplankton declines are projected to be greater than phytoplankton declines). When declining zooplankton densities are examined in relation to projected phytoplankton changes, we find that zooplankton declines exceed phytoplankton declines to a large degree. All models but three (CanESM2, GISS-E2-H-CC, and GISS-E2-R-CC) place such waters across much of the North Pacific excluding only subpolar waters, and in some cases equatorial and California Current upwelling waters. Projected declines in zooplankton exceed those of phytoplankton by 10 – 30% on average, with individual model maxima of 25 – 50% found along the periphery of the North Pacific subtropical gyre (NPSG).

Ecosystem impacts

Changes in predicted tuna and billfish species richness (*SR*) follow projected changes in epipelagic temperature. Across all models, the area of maximum *SR* shifts northward and eastward. Species richness declines across much of the central and western subtropics and increases in temperate and subpolar waters, with the magnitude of change increasing with distance toward the western tropical Pacific and temperate latitudes, peaking at approximately four species lost or gained (Fig. 2d). Most models project potential carrying capacity (K_p) for commercially valuable fish to decline by 20 – 50% across the North Pacific, or by roughly 2 – 5% per decade over the 21st century (Fig. 2e). As with trophic amplification, the areas projected to see the greatest declines in K_p are found along the periphery of the NPSG. Declining K_p is a result of both increasing epipelagic temperature and declining zooplankton density, with the primary driver varying across the North Pacific. In the western equatorial Pacific and NPSG declining zooplankton density has a stronger impact on K_p, while in the eastern equatorial Pacific and at temperate latitudes increasing epipelagic temperature is the stronger driver (Fig. 2f).

Discussion

The CMIP5 projections presented in this study suggest a number of changes to North Pacific pelagic habitat. Broadly, thermal habitat is projected to warm and be spatially redistributed. Zooplankton densities are projected to decline and to an amplified degree relative to phytoplankton declines. When these projections are examined more finely and in relation to one another, they suggest that commercial fisheries in the central North Pacific may see catch decline by 20 – 50% and be comprised of three to four fewer tuna and billfish species.

Changing pelagic habitat

While warming epipelagic temperatures might be expected to unfold as a straightforward poleward creep of present-day conditions, we find that this is not the case (Fig. 2a, d). Rather, warmer temperatures appear to emerge from the western equatorial Pacific and expand eastward and northward as moderate temperatures retreat in kind. Over time, this results in a reshaping of pelagic thermal habitat. For example, thermal habitat associated with adult tuna foraging is displaced by thermal habitat more commonly associated with tuna spawning grounds and spawning habitat is replaced by temperatures that exceed even the warmest temperatures associated with commercially valuable fish (Boyce *et al*., 2008; Lehodey *et al*., 2011, 2013).

Evidence suggests that fish and other pelagic organisms will relocate to maintain residence in preferred thermal habitat in both freshwater (Grenouillet and Comte, 2014) and marine (Pinsky *et al*., 2013; Montero-Serra *et al*., 2015) environments, and with relocations varying over different life history stages (Walsh *et al*., 2015). Some fish may simply be able to spend more time in deeper, cooler waters. However, such an adaptation comes at a cost. For example, fish may forage less successfully at the lower light levels found below the epipelagic realm. Organisms that are unable to exploit deeper habitat will be forced to relocate geographically. Such vertical and geographic relocations could ultimately alter predator – prey dynamics.

The emergence of new thermal habitat also raises questions, as it is projected to exceed current maximum temperatures. It remains unknown how or whether pelagic organisms will adapt to these temperatures. Storch *et al*. (2014) suggest there are firm limits on temperatures to which animals can adapt. They find that due to constraints posed by cellular complexity, the highest SST that allowed multicellular Eukaryea to grow was 40 °C, close to temperatures projected to occur over the North Pacific in our study. The unprecedented rate at which climate is changing (Doney *et al*., 2014) adds further uncertainty to questions surrounding adaptation.

In addition to changes in thermal habitat, we also project a shift towards lower zooplankton densities over the 21st century. Spatially, the lowest zooplankton densities are associated with the oligotrophic NPSG. Declining densities are manifested as both an expansion of the NPSG, as well as lower densities in NPSG waters (Fig. 2b). While we examine the oligotrophic NPSG from the perspective of zooplankton densities, our results are similar to those from other studies focused on phytoplankton that project the gyre's expansion (Sarmiento *et al*., 2004; Steinacher *et al*., 2010; Polovina *et al*., 2011; Cabré *et al*. 2015).

Not only do the models used in our study project zooplankton densities to decline across much of the North Pacific, but they also project these declines to be amplified relative to declines in phytoplankton densities. Stock *et al*. (2014) link trophic amplification to declining zooplankton growth efficiency as food resources (net primary production) decline, while Chust *et al*. (2014) link trophic amplification to nonlinear coupling of phytoplankton and zooplankton biomass. It remains unclear whether this amplification in the plankton community will propagate further up through the food web, however modeling work suggests that it will be amplified by some micronekton (Bell *et al*., 2013) and possibly throughout the size spectrum (Lefort *et al*., 2015). If trophic amplification does indeed carry through the food web, an amplification of roughly 20% at each trophic linkage could result in apex predator density (trophic level 4 – 5) declining by up to 50 – 60% by the end of the century, or by 5 – 6% per decade.

Ecosystem impacts of changing pelagic habitat

The projected impacts of climate change in the North Pacific extend beyond the immediate changes to temperature and food availability. Increasing epipelagic temperature is projected to lead to a redistribution of tuna and billfish *SR* (Fig. 2d). There is strong model agreement of a decline of up to 3 – 4 species across much of the subtropics with an increase of similar magnitude projected for temperate latitudes. These projected changes in *SR* largely, and not surprisingly given Eq. 1, mirror the changing footprint of thermal habitat in the North Pacific. Based solely on thermal tolerance, much of the subtropical North Pacific is projected to become less hospitable to adult commercially valuable tuna and billfish. While a decline of only a few species may not seem very substantial, the longline fisheries in these waters target only a small number of species, primarily bigeye tuna and swordfish (*Xiphias gladius*), and also catch several commercially-valuable, non-target species such as skipjack tuna, yellowfin tuna, shortbill spearfish (*Tetrapturus anguistorostris*), and striped marlin (*Tetrapturus audax*). Thus, even a small decline in *SR* could significantly impact catch composition, magnitude, and value. Likewise, at the northern limits of the fishery, the small increase in species diversity could potentially benefit fishermen. Whether this potential benefit would be offset by the increased expense of traveling further from port to fish is unknown. Fishermen may also shift their homeport based on target catch relocation, as some in the Hawaii-based longline fishery have already done.

Increasing epipelagic temperatures combined with largely declining zooplankton densities are projected to act together to lower North Pacific K_p over the 21st century. We find strong model agreement that K_p is projected to decline by roughly 20 – 50% across the North Pacific (Fig. 2e). Despite our measure of K_p being a simple relationship based on ecological theory, this projection is in line with previous studies that have projected similar declines in exploitable high-trophic-level biomass as the result of climate change (Lefort *et al*., 2015; Woodworth-Jefcoats *et al*., 2015). We also find that declines in K_p exceed those of zooplankton densities, further suggesting that trophic amplification in the plankton community may propagate up through the food web. Additionally, K_p is projected to decline even in regions where plankton densities are projected to increase (Fig. 2b, e). This suggests that potential increases in biomass at the base of the food web won't be enough to compensate for the metabolic costs of increasing temperatures. Further examination of the impact of temperature versus zooplankton on K_p shows that the dominant driver of change varies spatially (Fig. 2f). In subtropical regions where zooplankton declines are projected to be greatest, these declines seem to have the greater impact on K_p. In the eastern North Pacific and at temperate latitudes, waters seeing the greatest increase in epipelagic temperature, temperature increases drive K_p declines.

Potential carrying capacity is projected to decline most in and around the central North Pacific. This has the potential to particularly impact longline fisheries operating in this area. Potential fisheries yields could decline by up to 50% over a time when the Food and Agriculture Organization of the United Nations projects that food resources will need to increase by roughly 70% to meet the demands of a growing human population (UN, 2011). Such an increase in demand could further strain the ecosystem, as the heavy removal of large fish has the potential to drive down exploitable biomass independent of any bottom-up impacts (Blanchard *et al*., 2005; Ward and Myers, 2005; Polovina and Woodworth-Jefcoats, 2013).

The areas of greatest trophic amplification and declining K_p occur around the boundaries of the NPSG (Fig. 2c, e). To the north of the NPSG lies the North Pacific transition zone, a narrow area used as a migration and foraging corridor by a number of pelagic species (Polovina *et al*., 2001; Hazen *et al*., 2013). To the south of the NPSG are spawning grounds for a number of tropical tuna species (Lehodey *et al*., 2011, 2013). Thus, the areas likely to see the greatest declines in food availability are areas crucial to specific life history stages of pelagic species. Such a mismatch in resource demand and supply could amplify climate impacts on species exploiting these regions. Furthermore, given that organisms from around the North Pacific target these areas, changes here have the potential to impact the entire basin. These maxima of declining phyto- and zooplankton densities are not flanked by corresponding areas of increasing densities, suggesting that productive regions around the NPSG are not simply relocating. Or, if productive regions are relocating, they are still experiencing overall declines in phytoplankton densities. The importance of these regions bordering the NPSG, along with their relatively small size, makes them ideal areas for monitoring climate change as it unfolds. Survey (Howell *et al*., 2015; Polovina *et al*., 2015) and tagging (Block *et al*., 2011) efforts already in place in these regions may provide insight into how organisms across the food web are responding to climate change.

One question we are unable to address in this study is how regions bordering the NPSG may be impacted by changes in phenology. The transition zone in particular moves meridionally with the seasons. The phenology of both the seasonal migration of the transition zone (Hazen *et al*., 2013) and its associated productivity (Polovina *et al*., 2011) may change as a result of climate change. Thus, organisms targeting the region at specific times of the year may have to migrate farther or to different locations. Both finer temporal resolution projections and tagging data may help address such phenology questions.

Caveats

Our study focuses on the two primary influences on ecosystem capacity, temperature and food availability. These are far from the only influences, though. Other variables such as oxygen concentration, pH, and exploitation can influence pelagic carrying capacity. Given that changes in many of these variables are projected to have negative impacts in the North Pacific (Koslow *et al.*, 2011; Bopp *et al.*, 2013), they are likely to exacerbate the impacts of warming temperatures and declining food availability.

We also assume that physical climate influences will be the primary determinants of ecosystem capacity. However, species and trophic interactions are also influential. In some cases, these interactions can have a larger impact than physical climate drivers (Grenouillet and Comte, 2014; Ockendon *et al.*, 2014). Additionally, changes in temperature and food availability can alter foraging range and create new competition (Bond and Lavers, 2014). Such changes in predator – prey interactions could have large impacts on commercial fisheries and could potentially be examined through species-based ecosystem modeling approaches and network theory.

In this study we examine only the epipelagic realm, though many commercially valuable fish also inhabit mesopelagic depths (Howell *et al.*, 2010; Abecassis *et al.*, 2012). Future impact studies could examine a broader vertical habitat range. For example, Lefort *et al*. (2015) suggest that fishes able to migrate between epi- and mesopelagic depths may fare better in the face of climate change than fishes restricted to either realm. Finally, we examine only one climate change scenario. By examining RCP8.5, we hopefully project the upper limits of potential climate change impacts. Future work could examine more optimistic RCPs, potentially providing motivation to take mitigating actions by presenting goals for limited impacts.

Commercial fishery impacts of changing pelagic habitat

Through examining a suite of CMIP5 earth system models we find that climate change may significantly alter North Pacific epipelagic habitat over the 21st century. Warming thermal habitat and declining zooplankton densities are projected to lower potential carrying capacity, and in turn fishery yield, by approximately 2 – 5% per decade. Additionally, based on changing thermal habitat alone, species richness across much of the subtropics is projected to decline by up to four tuna and billfish species by the end of the century. Together, these changes have the potential to significantly impact commercial fish catch in the North Pacific. Fishery managers can use these projections to place current yields and management actions in a broader climate-based context. For example, early warning thresholds for changing catch composition or yield could be based on projected climate impacts. Such strategic management plans would ensure that the ecosystem is not further stressed by unsustainable removals.

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Tables

Table 1: For each model, the SST and epipelagic temperature ranges that decrease in frequency, increase in frequency, and emerge by the end of the 21st century followed by the zooplankton density ranges that increase and decrease in frequency by the end of the century.

Model	**Sea Surface Temperature (°C)**			**Epipelagic Temperature (°C)**			**Zooplankton Density (g C m^{-2})**	
	Decreases	Increases	Emerges	Decreases	Increases	Emerges	Increases	Decreases
Canadian Centre for Climate Modelling and Analysis Earth system model[1] (CanESM2)	20.0 – 30.0	30.0 – 38.0	34.0 – 38.0	14.5 – 21.5	21.5 – 32.5	30.5 – 32.5	0.05 – 0.20	0.20 – 0.40
NOAA Geophysical Fluid Dynamics Laboratory Earth System Model Generalized ocean layer dynamics[2] (GFDL-ESM2G)	20.0 – 29.5	29.5 – 35.0	32.5 – 35.0	13.0 – 18.5	24.5 – 32.0	30.0 – 32.0	0.50 – 0.90	0.90 – 1.85
NOAA Geophysical Fluid Dynamics Laboratory Earth System Model Modular Ocean Model 4[2] (GFDL-ESM2M)	20.0 – 30.0	30.0 – 35.0	33.0 – 35.0	15.0 – 25.5	25.5 – 32.5	30.0 – 32.5	0.40 – 0.95	0.95 – 1.75
NASA Goddard Institute for Space Studies ModelE2 Earth System Model with carbon cycle coupled to the HYCOM ocean model[3, 4] (GISS-E2-H-CC)	22.0 – 30.0	30.0 – 34.5	32.0 – 34.5	17.5 – 23.0	23.0 – 32.5	31.0 – 32.5	0.00 – 0.10	0.10 – 1.00
NASA Goddard Institute for Space Studies ModelE2 Earth System Model with carbon cycle coupled to the Russell ocean model[3, 4] (GISS-E2-R-CC)	20.0 – 30.5	30.5 – 34.5	32.5 – 34.5	16.5 – 26.5	26.5 – 33.0	31.5 – 33.0	0.00 – 0.15	0.15 – 0.85
Institut Pierre-Simon Laplace Low Resolution CM5A[5] (IPSL-CM5A-LR)	21.0 – 30.0	30.0 – 36.0	32.5 – 36.0	15.5 – 26.0	26.0 – 34.0	30.0 – 34.0	0.30 – 0.45	0.60 – 1.10
Institut Pierre-Simon Laplace Medium resolution CM5A[5] (IPSL-CM5A-MR)	21.5 – 31.0	31.0 – 36.5	33.0 – 36.5	15.5 – 26.0	26.0 – 34.0	31.0 – 34.0	0.30 – 0.65	0.65 – 0.95
Institut Pierre-Simon Laplace Low resolution CM5B[5]	21.5 –	30.0 –	32.0 –	17.5 –	26.5 –	31.0 –	0.25 –	0.35 –

(IPSL-CM5B-LR)	30.0	35.5	35.5	24.0	32.5	32.5	0.35	0.70
Max-Planck-Institute für Meteorologie Earth System Model low resolution[6] (MPI-ESM-LR)	20.0 – 30.0	30.0 – 37.0	34.0 – 37.0	14.5 – 22.0	22.0 – 33.5	31.5 – 33.5	0.10 – 0.75	0.75 – 1.50
Max-Planck-Institute für Meteorologie Earth System Model medium resolution[6] (MPI-ESM-MR)	20.0 – 30.0	30.0 – 36.5	34.0 – 36.5	16.0 – 21.0	21.0 – 35.0	32.5 – 35.0	0.10 – 0.70	0.70 – 1.55
Meteorological Research Institute Earth System Model Version 1[7] (MRI-ESM1)	21.0 – 29.5	21.0 – 34.5	31.5 – 34.5	16.5 – 27.0	27.0 – 30.5	29.0 – 30.5	0.00 – 0.20	0.20 – 0.40

[1]Christian *et al*., 2010 [2]Dunne *et al*., 2013 [3]Romanou *et al*., 2014 [4]Schmidt *et al*., 2014 [5]Dufresne *et al*., 2013 [6]Giorgetta *et al*., 2013 [7]Yukimoto *et al*., 2011

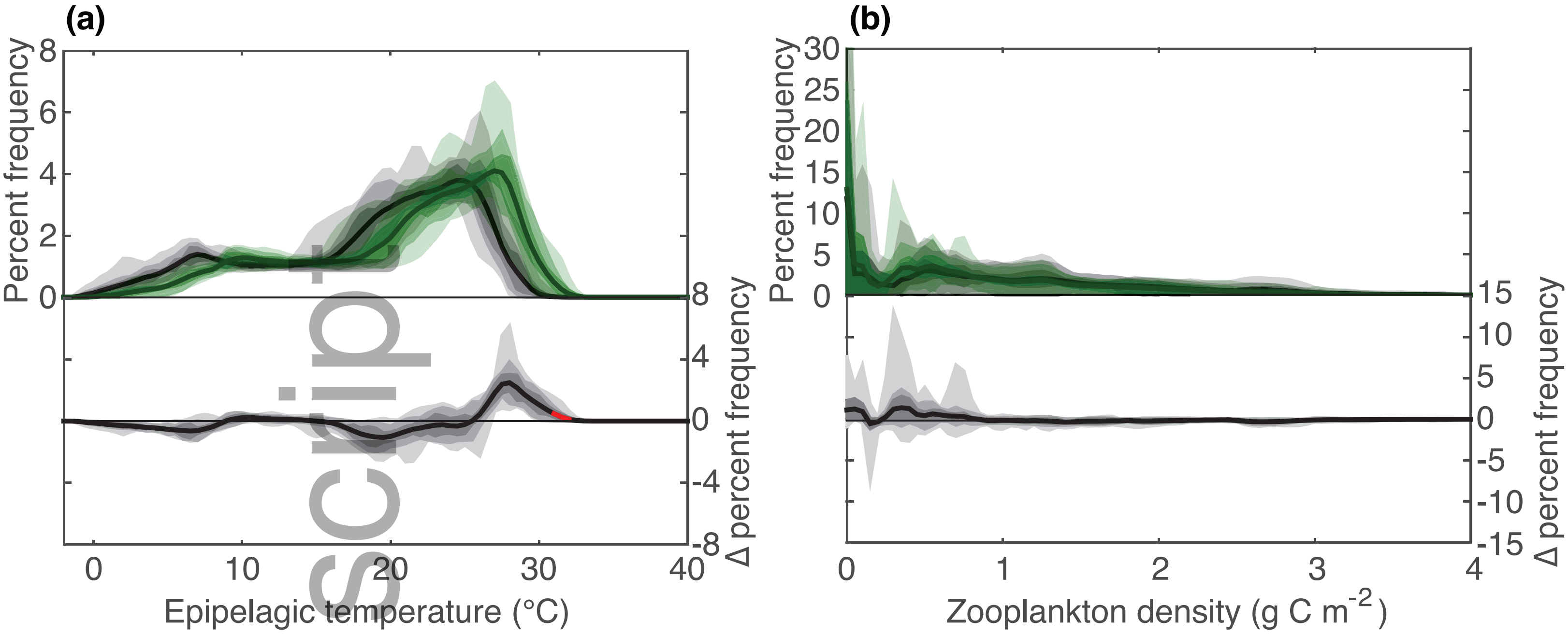
Table Caption

Table 1 For each model, the SST and epipelagic temperature ranges that decrease in frequency, increase in frequency, and emerge by the end of the 21st century followed by the zooplankton density ranges that increase and decrease in frequency by the end of the century.

Figure Captions

Fig. 1 Percent frequency distributions of 20-year mean pooled epipelagic temperatures (a) and zooplankton densities (b) from the beginning (grey) and end (green) of the 21st century are plotted above the difference between the two distributions. Solid lines show multi-model means. Terciles encompassing 33%, 67%, and 100% of the models are shaded progressively lighter. The red line in the lower panel of (a) indicates the temperature range over which at least half the models project the emergence of new thermal habitat.

Fig. 2 Multi-model median projected change in epipelagic habitat (a – b) and resulting degrees of ecosystem impact (c – f) over the 21st century: projected change in epipelagic temperature (a) and zooplankton density (b), degree of trophic amplification (indicated by warm colors) or the difference between projected phytoplankton and zooplankton percent declines (c), projected change in tuna and billfish species richness over the 21st century for waters within the bounds of a positive solution to equation 1 (5 – 30 °C) (d), projected percent change in potential carrying capacity (e), and the difference in the strength of changing zooplankton density (warm colors) versus changing epipelagic temperature (cool colors) as drivers of change in potential carrying capacity (f). In (a – e) stippling indicates areas where at least 80% of the models used project a change of the same sign. In (f) stippling indicates areas where at least 80% of the models used indicate the same dominant driver.



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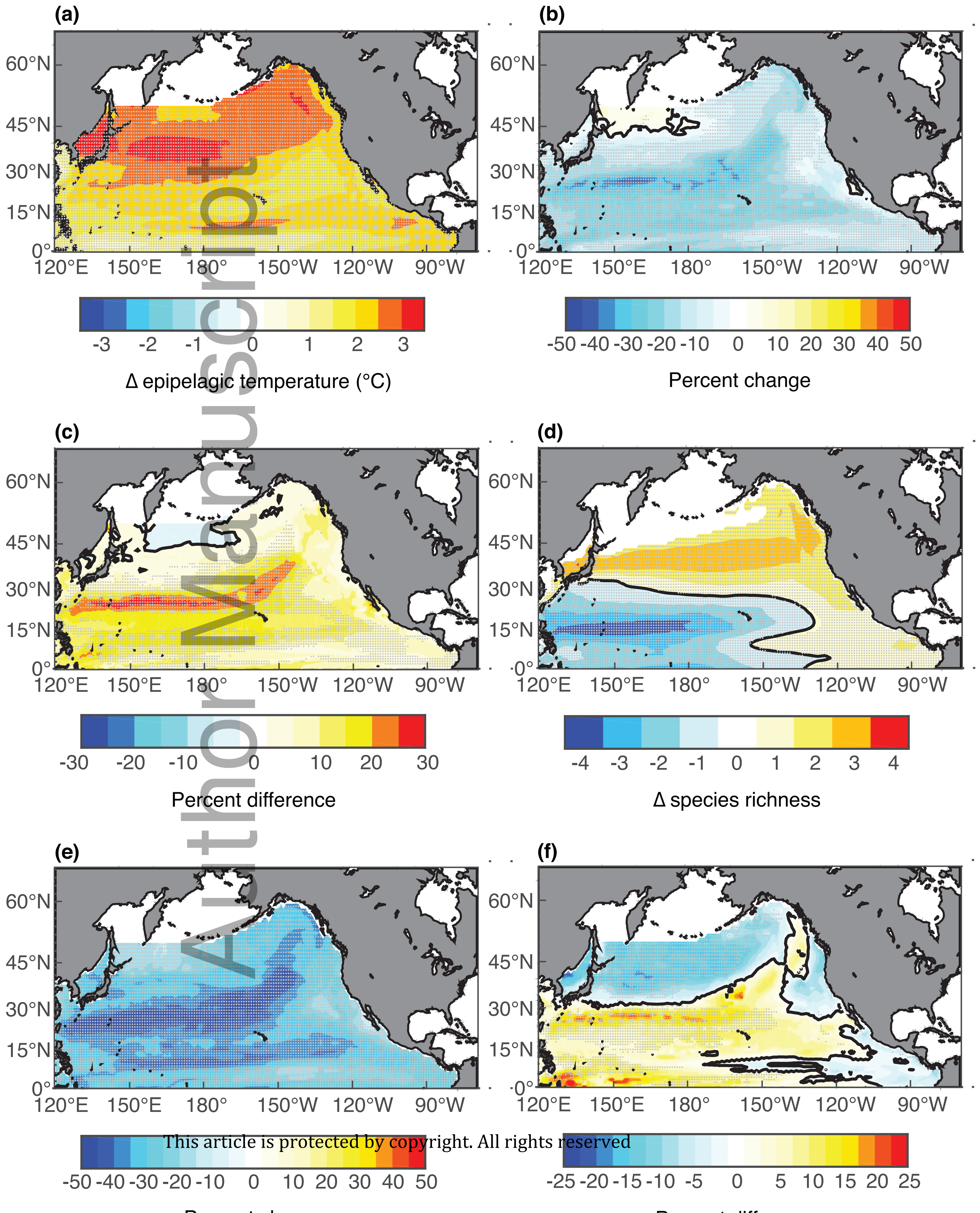
(a)
60°N
45°N
30°N
15°N
0°
120°E
150°E
180°
150°W
120°W
90°W
-3
-2
-1
0
1
2
3
Δ epipelagic temperature (°C)
(b)
-50 -40 -30 -20 -10
0
10
20
30
40
50
Percent change
(c)
-30
-20
-10
0
10
20
30
Percent difference
(d)
-4
-3
-2
-1
0
1
2
3
4
Δ species richness
(e)
-50 -40 -30 -20 -10
0
10
20
30
40
50
(f)
-25 -20 -15 -10 -5
0
5
10
15
20
25