Title: Ocean warming compresses the 3D habitat of marine life

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Summary*:* Vertical migration to reach cooler waters is a suitable strategy for some marine organisms to adapt to ocean warming. Here, we calculate that realized vertical isotherm migration rates (VIM) averaged -6.6+18.8 m decade^{-1} across the global ocean between 1980- 2015. Throughout this century (2006 – 2100), surface isotherms are projected to deepen at an increasing rate across the globe, averaging -32.3 m decade^{-1} under the RCP8.5 ‘business as usual’ emissions scenario, and -18.7 m decade^{-1} under the more moderate RCP4.5 scenario. The vertical redistribution required by organisms to follow surface isotherms over this century, is 3 - 4 orders of magnitude less than the equivalent horizontal redistribution distance. However, the seafloor and the depth of the photic layer pose ultimate limits to the vertical migration possible by species. These limits will be reached by the end of this century across much of the ocean leading to a rapid global compression of the 3-D habitat of many marine organisms. Phytoplankton diversity may be maintained but

compressed toward the base of the photic layer, whereas highly productive benthic habitats, especially corals, will have their suitable 3-D habitat rapidly compressed.

Main Text

Introduction

The effects of ocean warming on marine life are often summarized as a poleward displacement of their biogeographical ranges tracking the direction and horizontal velocity of surface isotherms in the ocean[1–4]. The assumption underlying this 2-dimensional depiction of warming effects on marine life is that surface temperature adequately represents the thermal regimes experienced in the upper ocean. However, climate velocity is defined as the rate and direction that isotherms shift through space[1,2,5], including the vertical dimension. Indeed, the upper ocean environment is 3-dimensional, with temperature and light, among other key factors, regulating biological activity at depth[6]. Consequently, species abundance and richness declines rapidly with depth[7].

Ocean warming involves the penetration of excess heat in the water column, which can now be detected down to characteristic depths of 700m across the upper ocean[8], thereby affecting horizontal thermal regimes, but also those at depth. Indeed, marine species around the USA have shifted their distribution, tracking the velocity of isotherm displacement along both the meridional and depth axis[5]. Similarly, North Sea demersal fish assemblages have shifted their depth distribution downwards in response to warming[9]. Hence, there is evidence that options of marine life to respond to warming do not only involve local acclimation or poleward range shift, but also shifting their 3-D range, to occupy deeper, cooler environments which are closer to their optimal thermal range.

The horizontal velocity of climate change and associated poleward displacement of marine life, have already been examined globally [1,2,4]. However, the vertical velocity of climate change with depth has not been reported at the global scale as yet. Available evidence from regional studies shows that the vertical velocity of climate change can be significant, with thermal envelopes deepening by up to 60 m decade^{-1} around the USA[5]. Deepening of vertical distributions over a few meters per year has been proposed as a mechanism for marine life to keep pace with climate change[4], analogous to increasing elevational ranges by terrestrial organisms[10] and easier than displacing their horizontal biogeographical ranges over tens of kilometers per decade. However, in the same way that marine life encounter limitations for their poleward range displacement with climate change, such as the presence of land masses in semi-enclosed seas [1,2], marine life can also meet constraints in their capacity to displace their range with depth. The restrictions to the vertical extent of organisms include, bathymetric boundaries in shallow coastal areas, light limitation for primary producers, depth-restrictions of resources and habitat availability and the presence of shallow oxygen minimum zones for animals [11]. All these factors set restrictions on the depth limit possible for vertical migration as a mechanism to adapt to ocean warming.

Here we examine the realized and projected vertical velocity of climate change across the global ocean through the analysis of vertical isotherm migration rates (VIM, m decade^{-1}) and discuss the potential impact of depth penetration of warmer regimes on marine life. We do so based on an ocean reanalysis available for the period 1958-2015 [12] and the CMIP5 ensemble of global climate models[13] available for the period 1950-2100 (thus covering present and future climate). We then examine evidence for the predicted displacement of the depth ranges of marine species, the constraints limiting vertical displacement and the consequences for the compression of the depth ranges of these species by the end of century under the RCP8.5 emission scenario - the scenario most closely representing current "*business as usual*" emission trajectories, and the RCP4.5 emission scenario - representing a moderate emission scenario broadly consistent with the Paris Agreement.

Results

Realized and projected rates of vertical isotherm migration

Realized VIM in the period 1980- 2015 averaged (±SD) -6.6±18.8 m decade^{-1}, ranging from deepening surface isotherms at -17.7±7.8m decade^{-1} across 69.9% of the ocean surface to rising isotherms at 19.4 ± 7.7 m decade^{-1} leading to surface cooling across 30.1% of the ocean surface (Fig. 1a). These large values in the recent decades are induced by a combination of global warming and natural climate oscillations (i.e. ENSO). Under a business as usual scenario, VIM projected for the period 2006-2100 averages -32.3m decade^{-1}, with negative velocities occurring throughout the global ocean, ranging from -3.8 m decade^{-1} to more than -40 m decade^{-1} along the Antarctic circumpolar current (Fig. 1b). Under a moderate emissions scenario (RCP4.5), the global average VIM is projected to be - 18.7 m·decade^{-1} with values ranging from -2.6 m decade $^{-1}$ to more than -30 m·decade^{-1} (Extended Fig 1). These results reflect the fact that average temperatures along the 21st century will be warmer, even if experiencing oscillations, than those observed at the end of 20th century. Projected fast VIM hot-spots are prevalent in both polar oceans as well as ocean regions adjacent to major current systems, such as the Gulf Stream and the Kuroshio current (Fig. 1b). The slowest VIM values are projected to extend offshore of the major eastern boundary upwelling regions, both in the E. Pacific and the E. Atlantic (Fig. 1b), a feature that is conserved across most global climate models (Supplementary Fig. 1).

The spatial patterns of VIM reflect the combination of warming patterns (Extended Fig 2a) with the pattern of thermal vertical gradients (Extended Fig 2b). High VIM values in the Southern Ocean and the tropical Pacific are mainly induced by the relatively low vertical temperature gradients (i.e. a long distance must be travelled in the vertical to compensate for the surface warming). Conversely, the high VIM values adjacent to major current systems are driven by higher than average warming rates. The projected depth penetration is consistent across all of the isotherms examined, with the 30^{o}C isotherm approaching the thermal limits of corals and other vulnerable tropical organisms to warming, spreading and deepening fast across the tropical and subtropical ocean (Extended Data Fig. 3). VIM rates are projected to be fastest at the Eastern Siberian Sea and Central Arctic large marine ecosystems (Supplementary Table 1). The ratio of projected horizontal (HIM, m decade^{-1}) to vertical isotherm migration under RCP8.5 averaged 5,900:1, and ranged from about 1,000:1 to about 30,000:1, with lowest ratios at high latitude (Fig. 1c), where VIM is fastest and HIM slowest (Extended Data Fig. 4). HIM/VIM ratios under RCP4.5 are similar to the ones obtained under scenario RCP8.5, due to a similar reduction in both HIM and VIM rates under moderate emissions scenarios (Extended Data Fig. 4).

Based on projected VIM under RCP8.5 and assuming the depth of the photic layer remains unchanged (Supplementary Fig. 2), present thermal regimes at the surface will reach the base of the photic layer within 87.1± 46.9 years, ranging from 5-10 years in the polar regions and north to the Kuroshi and Gulf Stream, to 140 years in the center of the sub-basins at subtropical latitudes (Fig. 1d). Under RCP4.5 the time required to reach the base of the photic layer would be 130.1 ± 51.1 years (Extended Data Fig. 1b). This provides an indication of the future compression of the 3-D habitats of photosynthetic organisms that are currently challenged by surface thermal regimes.

Implications for 3-D habitat compression

Two dimensional analyses of the response of marine life to ocean warming (e.g. [4,14–16]) often ignore the possibility that organisms may find refuge at depth, although this possibility has been acknowledged[17]. For instance, some works predicted a major reduction in phytoplankton potential diversity at low latitudes and an increase in diversity at high latitudes[14], but their 2-D approach assumed the surface temperature regime to apply throughout the photic layer that phytoplankton occupy. Combining the model applied by Thomas et al. [14]with the depth-resolved projected thermal regimes reported here, we show that phytoplankton can find refugia within the deep, cooler photic layer of the subtropical and tropical ocean (Extended Data Fig. 5), resulting in relatively conserved phytoplankton diversity (Fig. 2a and Extended Data Fig. 6). However, this requires a downward migration of species in those regions by, on average, -9.6 ± 6.4m by 2100 under scenario RCP8.5 compared to -4.7 ± 3.0 m under scenario RCP4.5. Indeed, whereas the potential diversity of polar phytoplankton increases (Fig. 2a), phytoplankton diversity in subtropical and tropical phytoplankton is largely conserved, but the habitat retaining this diversity is compressed toward the base of the photic layer (Fig. 2b). This is consistent with projections of the effect of warming of the subtropical and tropical ocean on picophytoplankton communities, which predict a redistribution toward increased abundance toward the base of the photic layer [18].

Highly productive benthic habitats (e.g. seagrass, corals and kelps) also have high light requirements and, therefore, face vertical compression of their available habitats when surface isotherms exceeding their upper thermal limits migrate down toward the maximum depth limits of these foundation species (Fig. 3, Extended Data Fig. 7, Extended Data Fig. 8). Hence, the habitat suitable to support kelps (e.g. thermal limit ∼ 26ºC; [19]), seagrass (thermal limit ∼25 - 36 ºC, depending on latitude, cf.[20]), tropical corals (thermal limit ∼30 ºC; e.g.[21]) and habitat-associated fish and invertebrates are also projected to become increasingly compressed toward their depth limit, as shallow populations will be increasingly exposed to thermal regimes above their tolerance limits (Extended Data Fig. 7, Extended Data Fig. 8). Depth-compression of organisms occupying benthic habitats is of particular concern, as it also involves a 2-D compression of the habitat of these organisms, which – unlike pelagic species – cannot occupy the full 3-D extent of the water column, since the area potentially occupied by these organisms is progressively pushed downslope. The projected timeline of habitat loss is particularly severe for tropical corals reefs (Fig. 3), where about 50% of habitat in the Coral Triangle, for example, is predicted to be lost by 2025 under a business as usual scenario (Extended Data Fig. 9), consistent with observed rates of coral loss over the past decade [22]. Seagrass and kelps are approaching their thermal limits in some regions [23] and are increasingly impacted by marine heat waves (e.g.[19,24,25]). They are also light-limited toward their poleward distributional limit where thermally suitable habitats (i.e. where minimum temperatures are above their lower thermal limit) are in deep layers where light is limited. Nevertheless, seagrasses and kelps are expected to expand poleward with improved thermal regimes and ice loss [26].

Consistently, under a business as usual emission scenario, our results show a potential habitat gain toward polar regions of 3.3 % and 11.0 % respectively, which would partially compensate their projected habitat loss in warm regions of -8.6% and -20.6% in 2100, respectively (Fig. 3). However, tropical corals are generally limited to waters with minimum temperatures > 16^{o} - 20^{o}C, with a characteristic minimum temperature threshold of 18^{o}C [27], and may, therefore, expand poleward[4] where suitable light conditions are found [27]. A detailed assessment of potential locations where coral could establish would require an analysis of bottom substrates, but our models provide a first idea of potential expansion. In particular, they predict a 7.0 % habitat expansion of suitable coral reef habitat poleward of their current range with ocean warming, as the 18^{o}C minimum monthly temperature isotherm will penetrate to depths receiving sufficient light to support coral growth. Similar behaviour but at reduced rates is found under the moderate emission scenario (Fig 3, Extended Data Fig.9).

Consistency of realized rates of vertical velocity with reported changes in depth distributions of marine organisms

The prediction that warming-associated mortality will compress the 3-D extent of marine habitats (Fig. 3) is consistent with the reported effects of marine heat waves in the mortality of vulnerable benthic organisms (Supplementary Table 2). Seagrass diebacks during the past decade show mass mortality events have affected the upper range of the meadows (Supplementary Table 2), ranging from diebacks above 1 m depth in Chesapeake Bay [28] and Florida Bay [29], where depth limits are confined by shallow photic layers or bathymetry, respectively, to diebacks penetrating down to 15 and 25 m depth during marine heat wave events causing mass-mortality of seagrasses in Shark Bay (e.g. 2011 heat wave,[25,30]) and the Balearic Islands in the Mediterranean (e.g. 2003 heatwave, [24]). The W. Mediterranean heat-wave of 2003 was also reported to cause diebacks of soft corals down to 25-40 m depth[31], and the W. Australia 2011 marine heat wave caused mass mortality of kelps reaching down to 30 m depth[19]. While kelps in W. Australia live down to ∼60m,[32] the state of deeper populations in heatwave affected areas remains unclear.

Reports of coral bleaching and associated mortality during heat waves, such as the 2015-2016 global mortality event[22], have predominantly focused on shallow reefs, with little reference to the condition of deeper habitats ([22,33]). Similarly, 2-D projections of future thermal stress for coral reefs predict more frequent mass bleaching events for the world's reefs[34] but do not address the depth-penetration of thermal regimes causing coral mortality. Where bleaching events on corals have been observed across a depth gradient, bleaching rates were generally lower on deep reefs compared to shallow reefs, despite thermal stress causing significant coral mortality down to depths of 40m [35]. Depth refuges on the GBR were observed to be temporally constrained by warm water penetrating into deeper depths on some years, resulting in thermal bleaching. Moreover, lower diversity on mesophotic reefs suggests that depth refuges may not support as many species as currently observed in shallow environments [35]. Nevertheless, as isotherms penetrate deeper, these findings do broadly support the role of depth as a refuge for coral reefs, analogous to existing evidence of long-term poleward expansion of tropical reefs at 14 km year^{-1} in Japan[36,37] and eastern [38] and western Australia[39].

There are, however, limitations in using impacts of recent heat waves as proxies of organismal responses to future, gradual warming. Extreme events, such as heat waves, sieve populations, removing the most heat-sensitive genotypes, leading to surviving populations better adapted to warmer regimes. Currently, long-term adaptation is poorly represented in projections of climate change impacts [40,41]. Evidence from long-term time series of phytoplankton [42] and laboratory experiments by phytoplankton[43,44] and corals[45], suggest that acclimation and genetic adaptation to gradual warming may be possible for some vulnerable populations. However, laboratory experiments on adaptation of short-lived phytoplankton species to warming have also shown that adaption comes with trade-offs that may affect the performance of the adapted population [44].

The vertical isotherm migration hotspots identified encompass important regions for biodiversity and climate change. For example, vertical isotherms in the Coral Triangle are projected to deepen by ca. 30-40 m decade^{-1} (Fig. 1b, Extended Data Fig. 7, Extended Data Fig. 8). This region is a global hotspot for biodiversity[46] and vulnerable to warming, with species living close to their thermal limits[47] and current warming rates of 0.09-0.12 °C decade^{-1}. The vulnerability of organisms in the Coral Triangle is evidenced by severe coral bleaching in the past two years[33]. Our results suggest that potential depth refugia for organisms in this region may be ephemeral due to fast isotherm deepening rates. Indeed, the 30°C isotherm is projected to reach the depth limit of suitable coral habitat by year 2040, on average in this region (Fig 1d, Extended Data Fig. 7, Extended Data Fig. 8). Eastern continental margins of Australia, South America and Southern Africa also represent hotspots of vertical isotherm migration. Fast deepening rates in these regions coincide with strong poleward-flowing boundary currents, with the capacity to facilitate horizontal migration of species[48]. The potential for poleward horizontal migration in these regions may, therefore, offset the physiological challenges associated with vertical migration (e.g. light, hydrostatic pressure, oxygen-limitation capacity). At the same time, south-eastern Australia, for example, is warming four-fold faster than mean global ocean warming rates [49], and benthic species there are already living on the poleward edge of the continental land mass, thereby limiting the habitat available for further poleward migration. These species are faced with a double jeopardy, as they are unable to respond to climate change through either horizontal or vertical migration.

Discussion

The results presented here confirm the acknowledged but hitherto overlooked importance of considering the vertical migration of isotherms when evaluating constraints to the capacity of marine life to adapt to surface warming by displacing their range at depth. Hence, current understanding, dominated by 2-D analyses of biotic responses to ocean warming [1,4,14,34], need be substantially reconsidered when vertical displacement of isotherms is considered. For instance, predicted losses of phytoplankton biodiversity in the tropics are not supported when considering the existence of thermal refugia toward the base of the photic layer. However, our analysis point to a rapid global compression of the 3-D habitat of marine organisms associated with benthic photosynthetic habitat-forming organisms. The capacity of these organisms to adapt to warming by vertically displacing their range is constrained by the depth of the photic layer while bathymetric limits also involve the 2-D compression of their range as they are displacing toward deeper waters tracking vertical migration of suitable isotherms. In addition to light and bathymetry, the presence of waters cooler than lower thermal thresholds also confine the depth penetration of tropical organisms expanding their range poleward, which also limits the potential depth range occupied by corals expanding into temperate latitudes. Lastly, the expansion of the extensive shallow oxygen minimum zones in the ocean also contributes to further compressing the 3-D habitat of organisms unable to live in hypoxic layers, squeezing them between shoaling oxygen minimum layers (e.g.[50]) and deepening isotherms.

Our analysis shows that the depth of the photic layer poses an ultimate limit to the habitat compression possible for photosynthetic marine organisms and associated biota, consistent with available evidence of the depth-redistribution of species in response to warming. Projections of vertical isotherm migration rates under a business as usual scenario, range from -3.8 to more than -40 m decade^{-1} and reveal that 50% of the available 3-D biogenic habitat could be lost within 80-90 years. As such, depth refugia may only provide a short-term strategy for many species, for which poleward migration or rapid thermal adaptation to keep pace with "*business as usual*" warming rates may be the only option. Moreover, unless phytoplankton communities will be dominated by thermally resistant species, there will be a 3-D compression of the habitat of photosynthetic organisms. In turn, this implies a general reduction in primary production, as light levels decline exponentially with organismal displacement at depth. The prevailing 2-D understanding of the responses of marine life to climate change needs to be expanded to 3-D approaches, integrating the vertical habitat compression of marine organisms with ocean warming. The evidence for ongoing and future widespread 3-D habitat compression of marine life represents a major, unrealized impact of climate change on marine ecosystems that requires urgent attention. This should be complemented by studies assessing the capacity for adaptation to new thermal regimes of different species, which can partially counteract the impacts of warming.

Materials and Methods

Data

The characterization of the 3-D temperature field for the present climate is done using the outputs from the ORAS4 reanalysis [12], available at https://www.ecmwf.int/en/forecasts/datasets/archive-datasets/browse-reanalysis-datasets) for the period 1958-2014. This reanalysis is based on the NEMO ocean model with 1° of horizontal resolution and 42 vertical levels. The model assimilates temperature and salinity in-situ profiles, along-track sea-level anomalies and sea-level trends.

For the projected evolution of the temperature field along the 21st century we have used the outputs from an ensemble of 28 Global Climate Models (GCMs, Supplementary Fig 1) from the CMIP5 project [13], available at https://cmip.llnl.gov/cmip5/data_portal.html) under the RCP8.5 and RCP4.5 scenarios of greenhouse gases emissions. The temperature change projected by each model has been computed as the difference between the mean temperature in the period 2075-2100 and 1980-2005. Then, those anomalies have been interpolated to the ORAS4 grid and added to the present temperature from ORAS4 in order to get the projected temperature. This procedure has been followed to remove potential biases in the GCM simulations [51]. For all the diagnostics used in this work, we have done the computations for each model and then averaged the outputs to get a more robust estimate of the future evolution of the diagnostics.

For the Mediterranean region, additional computations have been performed using high resolution regional reanalysis and regional climate models. The regional reanalysis used here is the CMEMS product (https://doi.org/10.25423/medsea_reanalysis_phys_006_004, [52]run at $1/16^{\circ}$ of horizontal resolution, 72 vertical levels and assimilating *in-situ* and satellite observations. The regional climate simulations have been obtained from the MedCORDEX initiative [53] and all of them had horizontal resolutions higher than $1/8^{\circ}$, which is considered to be enough to solve the most important processes in the region. The values shown in all the figures for the Mediterranean have been obtained from this regional ensemble. Nevertheless the final results using the high resolution products did not differ much from the global products.

The depth of the base of the photic layer has been obtained from SeaWifs satellite images. Monthly estimates downloaded from https://oceandata.sci.gsfc.nasa.gov/SeaWiFS/Mapped/Monthly/9km/Zeu_lee/ have been averaged for the period 1997-2010 to obtain a 12-month climatology.

The boundaries defining the Large Marine Ecosystems of the Worlds have been downloaded from http://lme.edc.uri.edu/.

Isotherm migration rates

The vertical isotherm migration rates (VIM) are computed assessing the speed at which the present sea surface temperature at a given location deepens due to global warming. To do so, for each location (x_0,y_0), we examined the projected 3-D temperature field at the same location ($T^{2100}(x_0,y_0 ,z)$) and we extracted the depth at which the present SST (x_0,y_0), is found (Z_{new}) using linear interpolation. Then, VIM, measured in m/year, is simply computed as:

$$\boldsymbol{VIM = (Z_{new})/(t_{end}-t_{ini})}$$

where t_{end} is year 2100 and t_{ini} is year 2006. Therefore, VIM reflect the averaged isotherm migration rate over the period 2006-2100 for each of the two scenarios. The values of VIM will depend on the local rate of warming and the shape of the temperature vertical profile. Thus, in areas with a strong thermocline, one can expect low VIM, while in regions with a weak thermocline, VIM will be large (i.e. the present SST will be found at large depths).

We have also computed the horizontal isotherm migration rates (HIM, Extended Data Fig. 4). In this case, for a given location (x_0,y_0), we look in the projected sea surface temperature field (SST^{2100} (x,y)) what is the closest location at which the present SST (x_0,y_0) is found (x_{new},y_{new}). The distance is computed as the minimum number of connected pixels between two locations, thus taking into account possible land barriers. Then, HIM, measured in m/year, is computed as :

$$HIM = d(x_{new},y_{new}, x_0,y_0)/(t_{end}-t_{ini})$$

where d(x_{new},y_{new}, x_0,y_0) is the distance between the new location (x_{new},y_{new}) and the original location (x_0,y_0).

The ratio HIM/VIM (Fig 1c) provides a measure of the comparison between two strategies for marine organisms to respond to global warming: the migration in the horizontal or in the vertical. Low HIM/VIM ratio indicate that a short vertical migration implies the same change in the thermal regime than a long horizontal migration. Sensitivity tests have been performed to see if VIM or HIM values changed depending on the month of the year used to do the computations, but no significant differences have been found.

Potential diversity of phytoplankton communities.

We followed the same approach as Thomas et al. [14] to estimate the potential diversity of phytoplankton communities. This is not the actual diversity as we do not know the relative abundance of each species in the community, but the potential diversity solely based on thermal niches. We used the thermal ranges and thermal optimal temperature for individual phytoplankton species Thomas et al. provide in the supplementary information [14] to identify the number of phytoplankton species that meet thermal conditions within their thermal range a particular location, defined here as a 1º by 1º cell within an ocean grid. We first did so using present sea surface temperature values, as Thomas et al. did [14] obtaining the same results they show (Extended Data Fig. 5a). We then considered that phytoplankton could establish at any depth inside the photic zone, and, therefore assessed, using the same approach, the number of phytoplankton species that met temperatures consistent with their thermal tolerance at any depth within the photic zone for each location. Using this 3-D approach we found a greater potential phytoplankton diversity in tropical and subtropical regions (Extended Data Fig.5b), as suitable thermal conditions may not be found in surface waters but maybe found in deeper waters within the photic layer. We used the same approach to project future potential diversity, using the projected 3-D temperature field.

We have also computed the averaged depth of the potential community. To do so, we have computed, for each phytoplankton species (*k*) and at each grid point, at what depth we find the temperature closest to its optimal temperature Z_k^{opt}. Then, the characteristic depth of the potential community is computed as the average of Z_k^{opt} for all the species that meet their thermal range within the photic layer at that location. The global distribution of calculated Z^{opt} for the present climate are shown in Extended Data Fig. 5c, and the projected changes in Fig 2b and Extended Data Fig. 6.

Suitable Habitats for benthic organisms

The suitable habitats for benthic organisms were defined using light and temperature criteria [54]. For each group (Coral, Kelp and Seagrass), the potentially suitable habitat is first defined as those locations at which a certain amount of radiation reaches the bottom. The minimum required radiation for those three groups was set to 1.4, 0.3 and 5.1 mol photons m^{-2} d^{-1}, respectively, which represent the minimum irradiance to support these communities [54]. We then also imposed the condition that the temperature at the bottom should be below their thermal limit (30^{o}C for tropical corals, 26^{o}C for Kelp and 25 - 36^{o}C, depending on latitude, for seagrass, cf.(22)). The use of light and temperature thresholds to define the suitable habitat for benthic organisms delineate a maximum potential extent, as it ignores other limiting factors, such as adequate substrate, for which global distribution is not available. These analyses assume that the depth of the photic layer does not change consistently with warming in the coastal ocean. Whereas we cannot rule out such changes, recent evidence reports no clear evidence of long-term trends [55].

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Author contributions: Study conception (GJ, CMD, NM, SB, SA), Data collection (SA, NM, SB, JS-G), Computation and formal analysis (GJ), Manuscript Writing and Reviewing (CMD,GJ, NM, SA, SB, JS-G).

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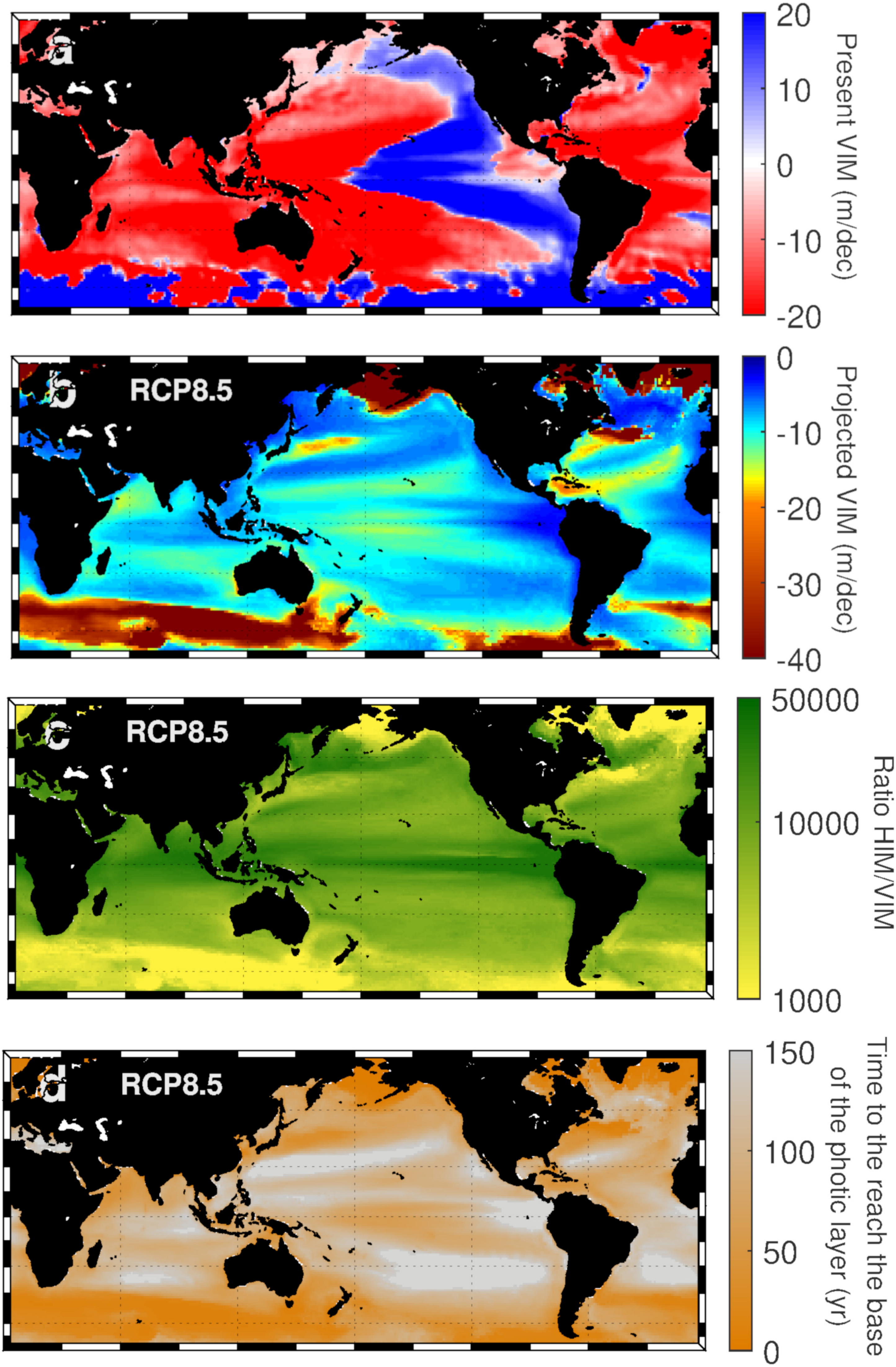
Materials and correspondence: Correspondence and material requests should be addressed to gabriel.jorda@ieo.es

Figures

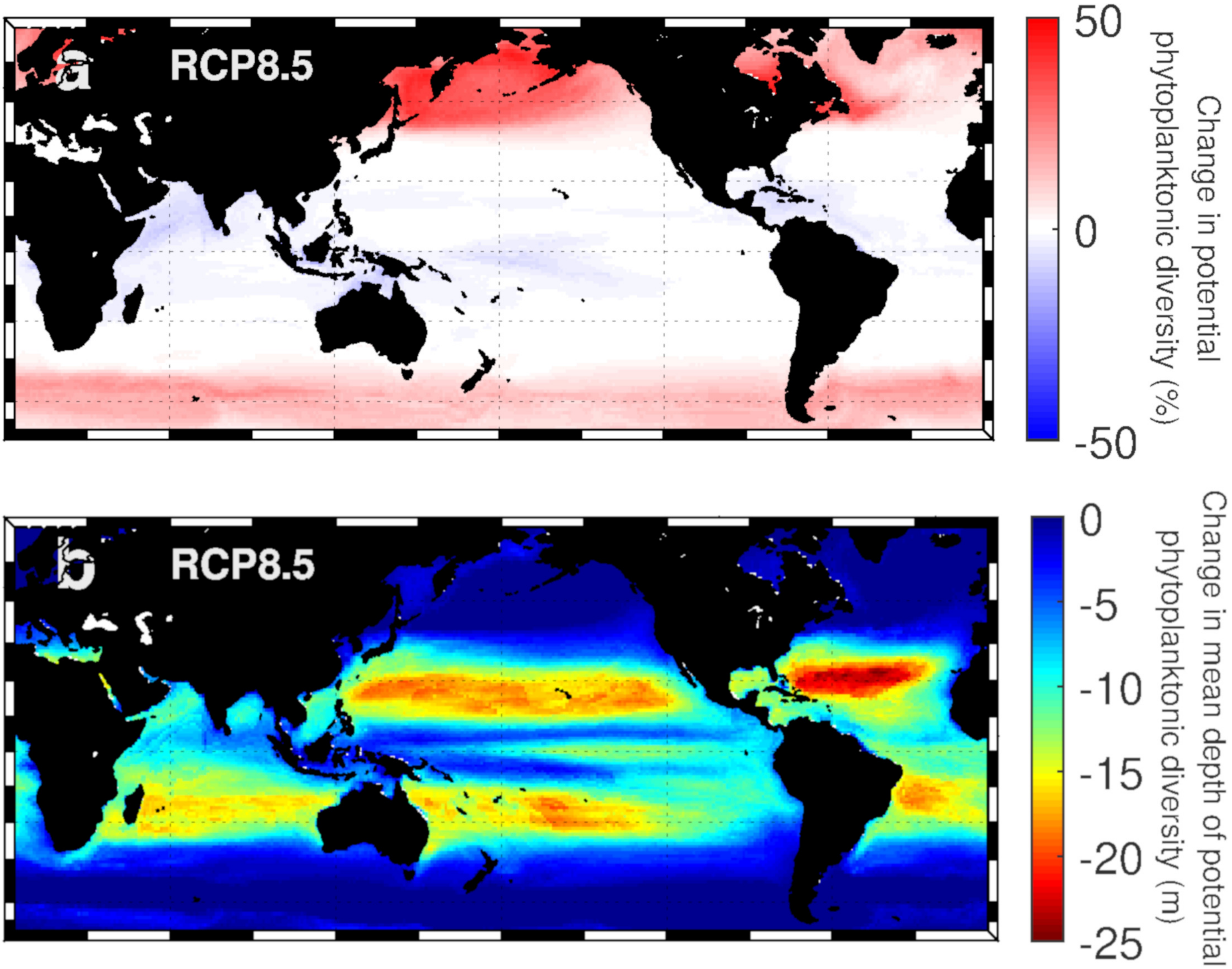
Figure 1: **Description of isotherm migration.** (A) Realized vertical isotherm migration rate (VIM) (m/dec) for the period 1980-2015 (B) Projected VIM (m/dec) for the 21st century under the RCP8.5 scenario (C) Log ratio of horizontal over vertical isotherm migration rates (D) Time estimated for the present sea surface temperature to reach the base of the photic layer across the ocean (in years).

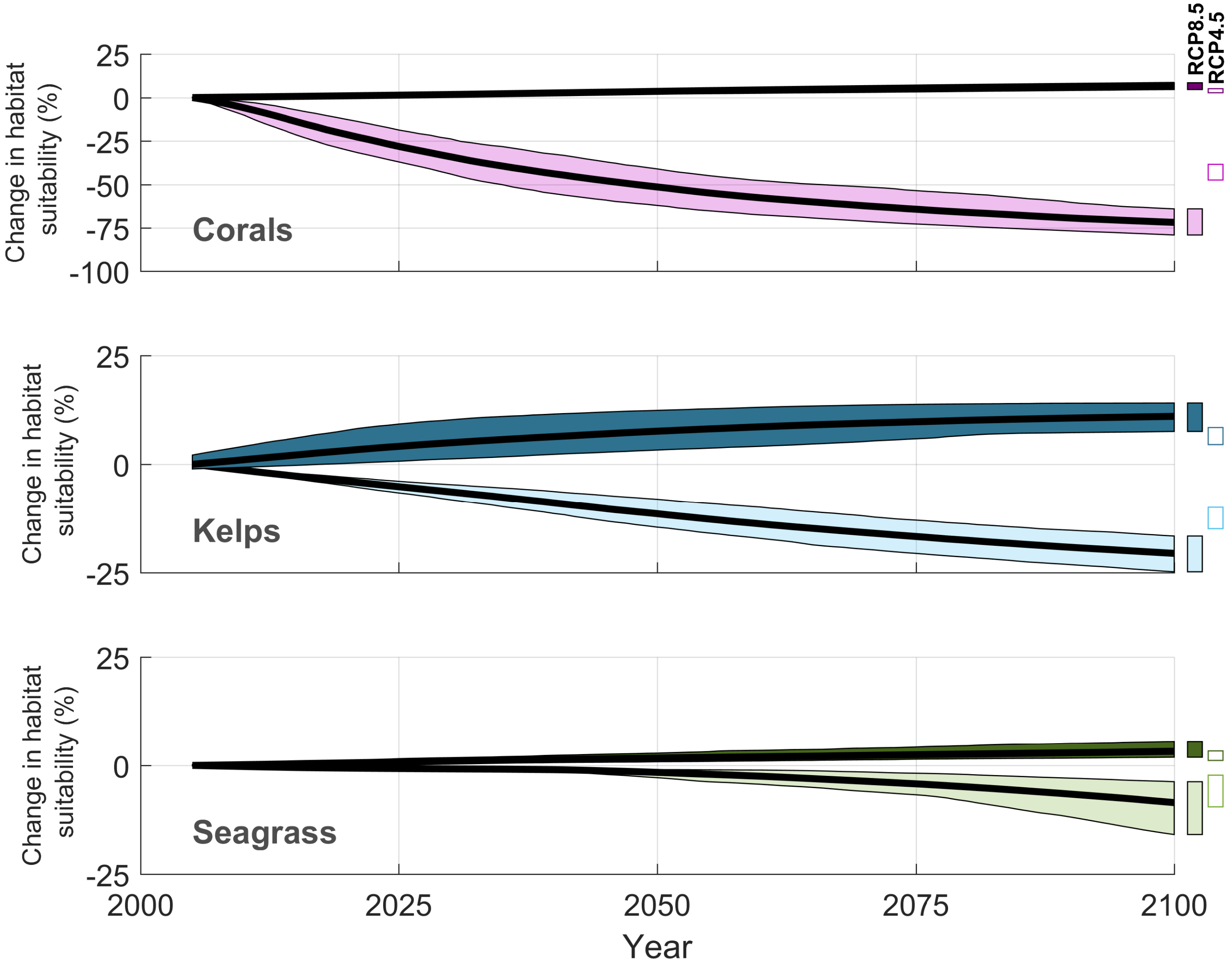
Figure 2: **Changes in potential phytoplankton diversity** under RCP8.5 emissions scenario. (A) Percent change in potential diversity between historical and projected future temperature regimes considering 3-D habitats. (B) Change in the mean depth (in meters) of potential phytoplankton communities between present (1980-2005) and end of the 21st century (2075-2100).

Figure 3: **Changes in the suitable habitats for benthic organisms.** Light colors show the projected change of present suitable habitat for corals (A), kelp (B) and seagrass (C) due to 3-D habitats compression during the 21st century (expressed as a % of present conditions) under the RCP8.5 scenario. Dark colors show the fraction of new suitable habitat for these benthic organisms that will appear in areas too cold to support these habitats at present due to global warming. The bars in the right express the range of values for scenarios RCP8.5 and RCP4.5. Note the different vertical axis in each panel.

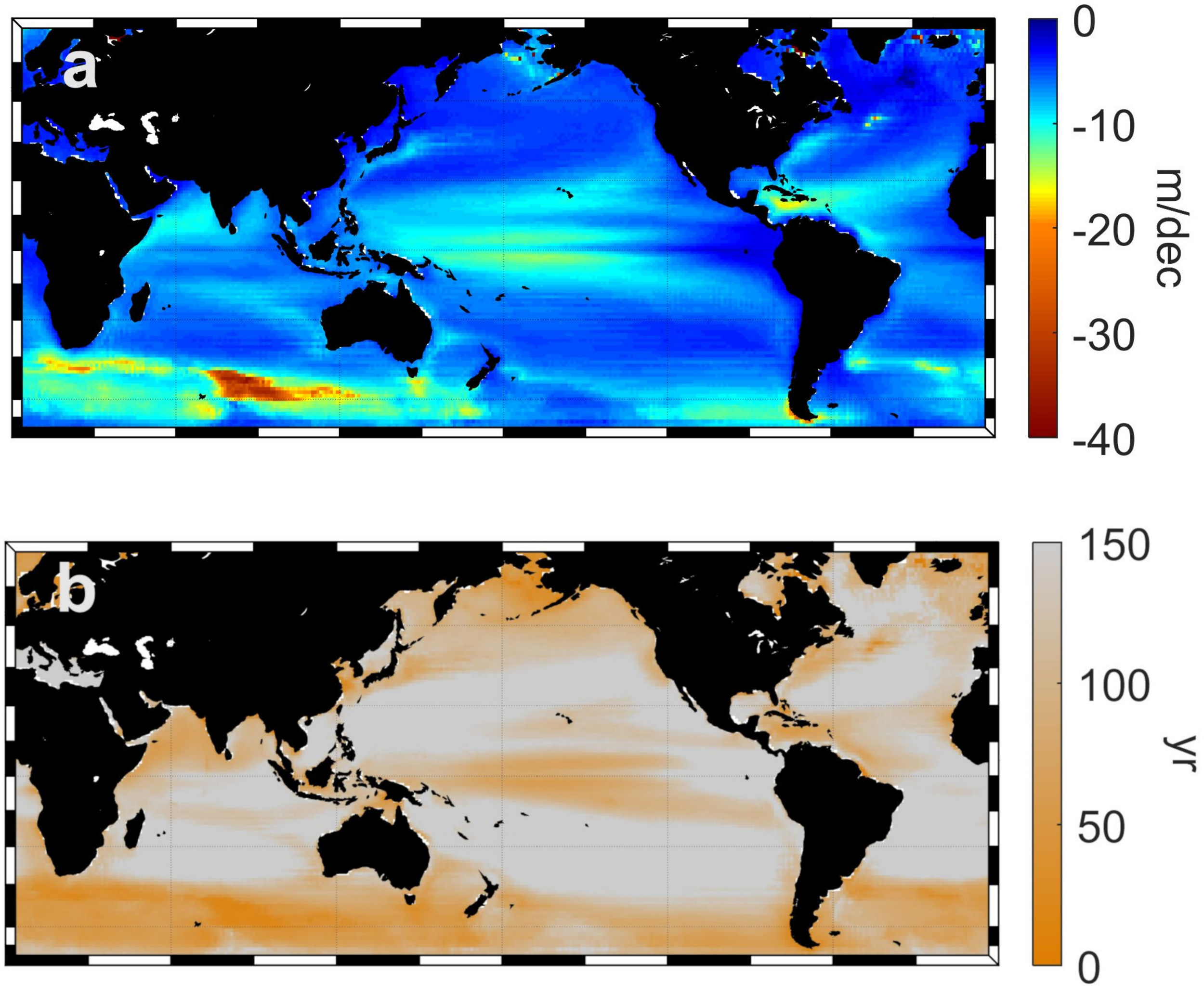


a
Present VIM (m/dec)
20
10
0
-10
-20
b
RCP8.5
Projected VIM (m/dec)
0
-10
-20
-30
-40
c
RCP8.5
Ratio HIM/VIM
50000
10000
1000
d
RCP8.5
Time to the reach the base of the photic layer (yr)
150
100
50
0

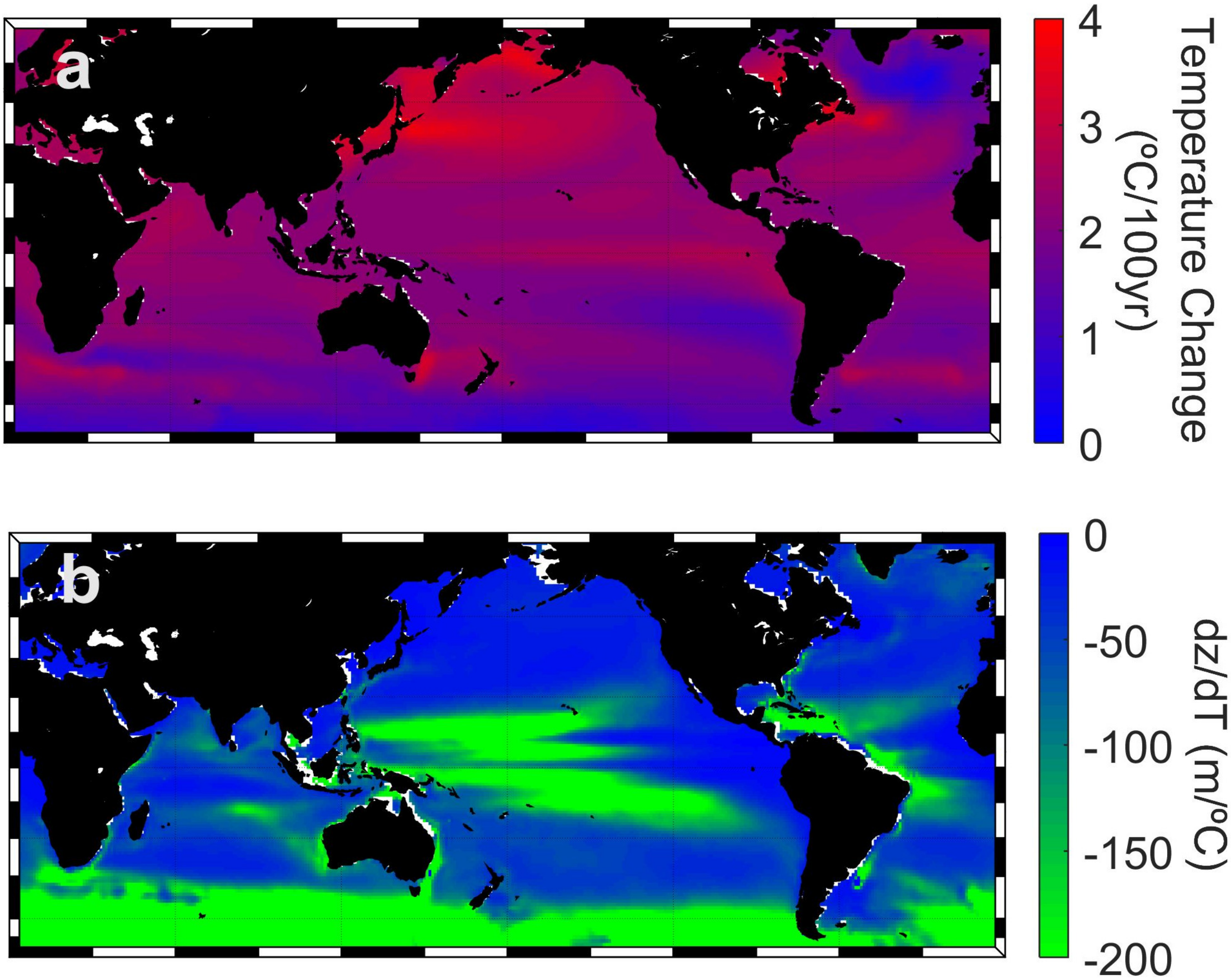

a
RCP8.5
50
0
-50
Change in potential phytoplanktonic diversity (%)
b
RCP8.5
0
-5
-10
-15
-20
-25
Change in mean depth of potential phytoplanktonic diversity (m)



RCP8.5
RCP4.5
25
0
-25
-50
-75
-100
Change in habitat suitability (%)
Corals
Kelps
Seagrass
2000
2025
2050
2075
2100
Year

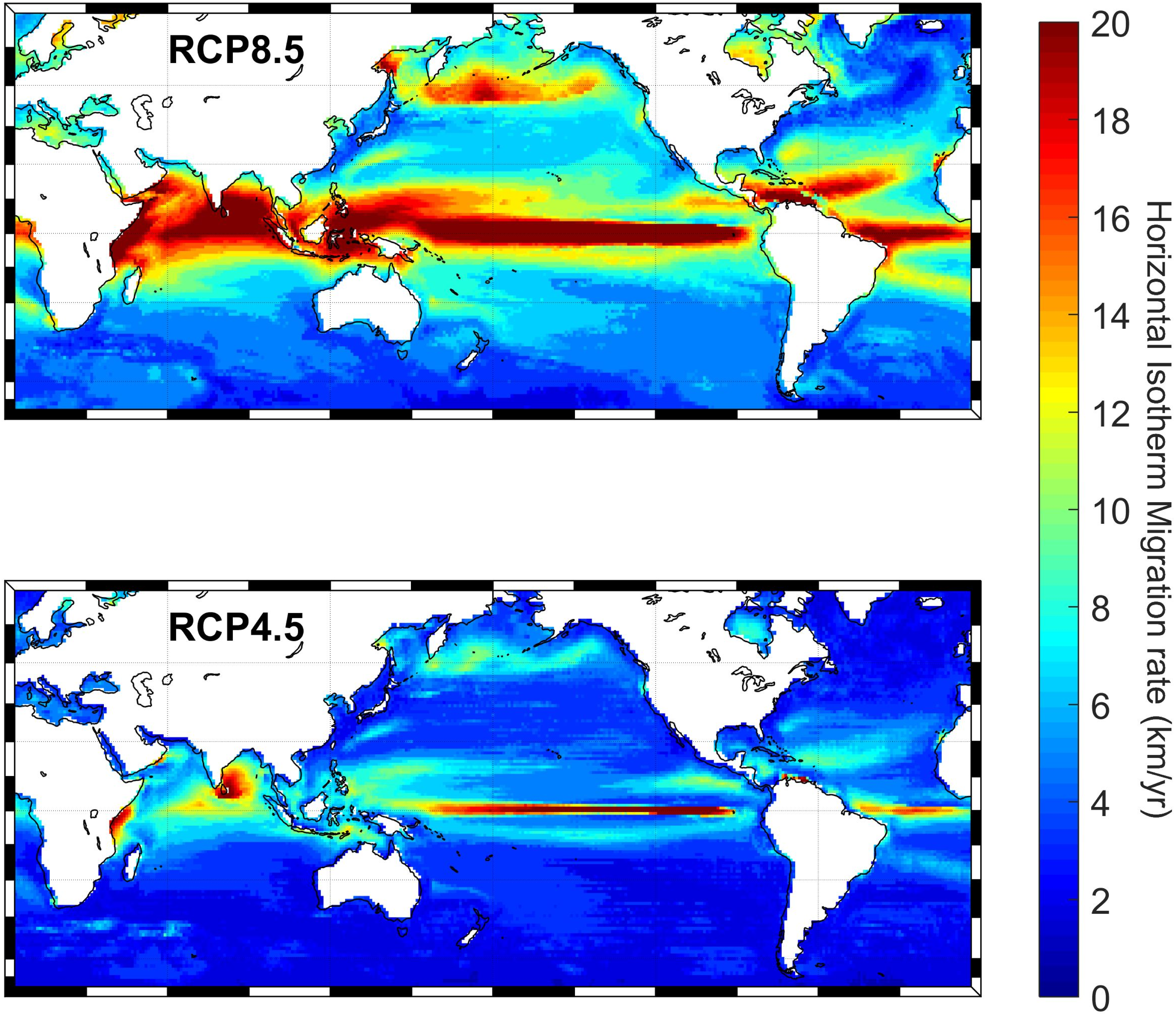


Time to the reach the base of the photic layer under RCP4.5

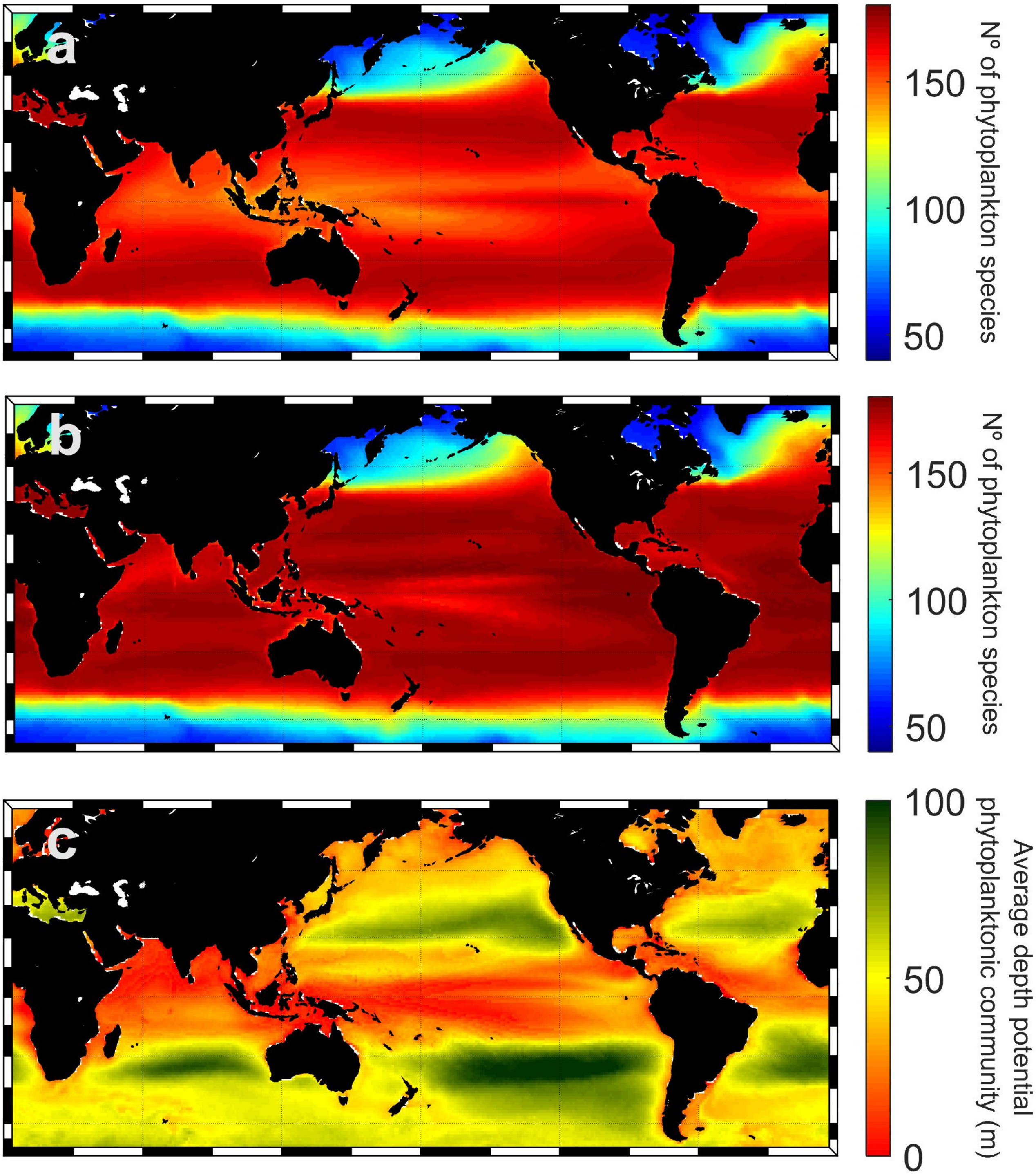


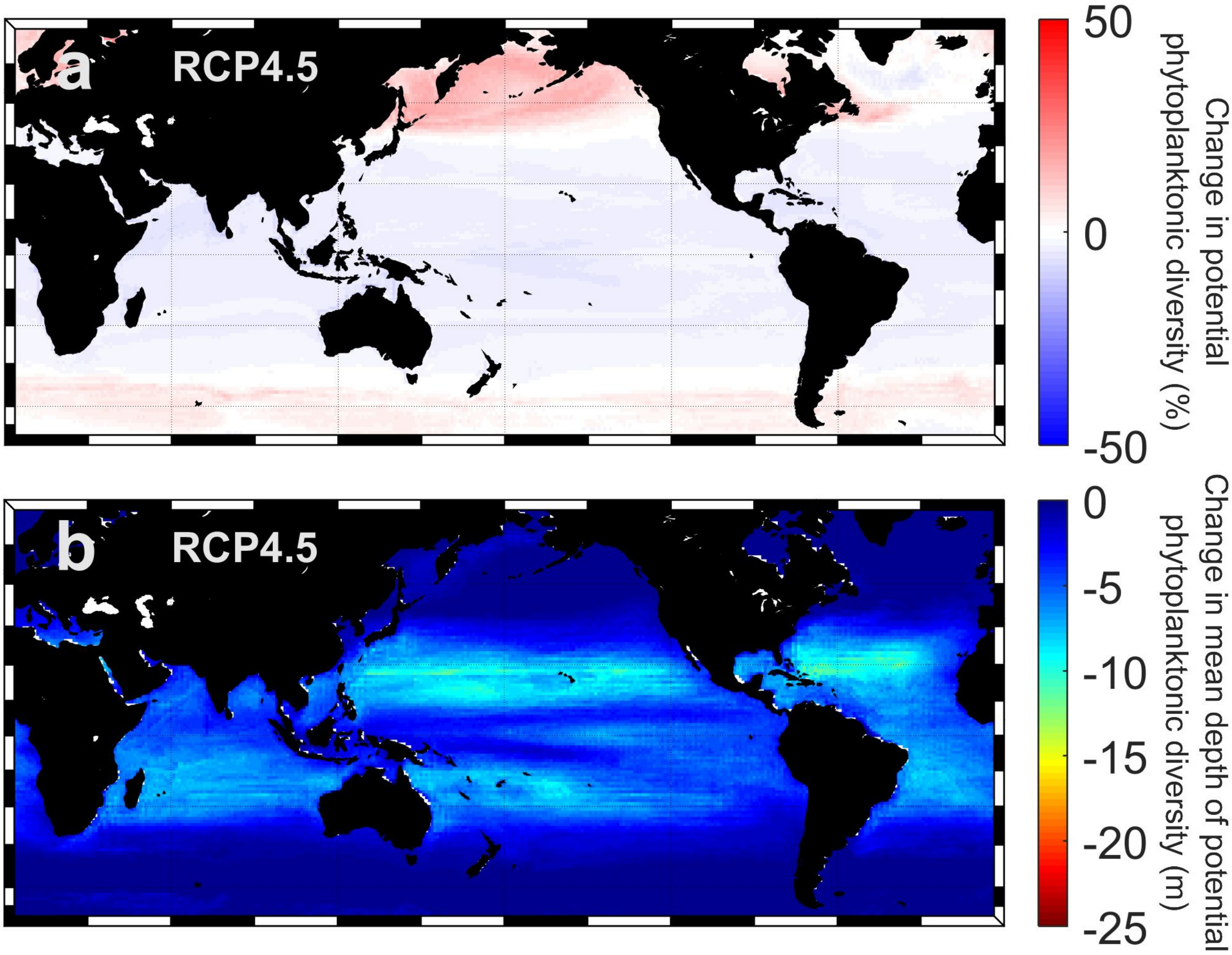
a
Temperature Change (°C/100yr)
4
3
2
1
0
b
dz/dT (m/°C)
0
-50
-100
-150
-200

PRESENT CLIMATE
RCP8.5
RCP4.5
20ºC Isotherm
25ºC Isotherm
30ºC Isotherm
depth (m)
300
150
0
depth (m)
150
75
0
depth (m)
80
40
0



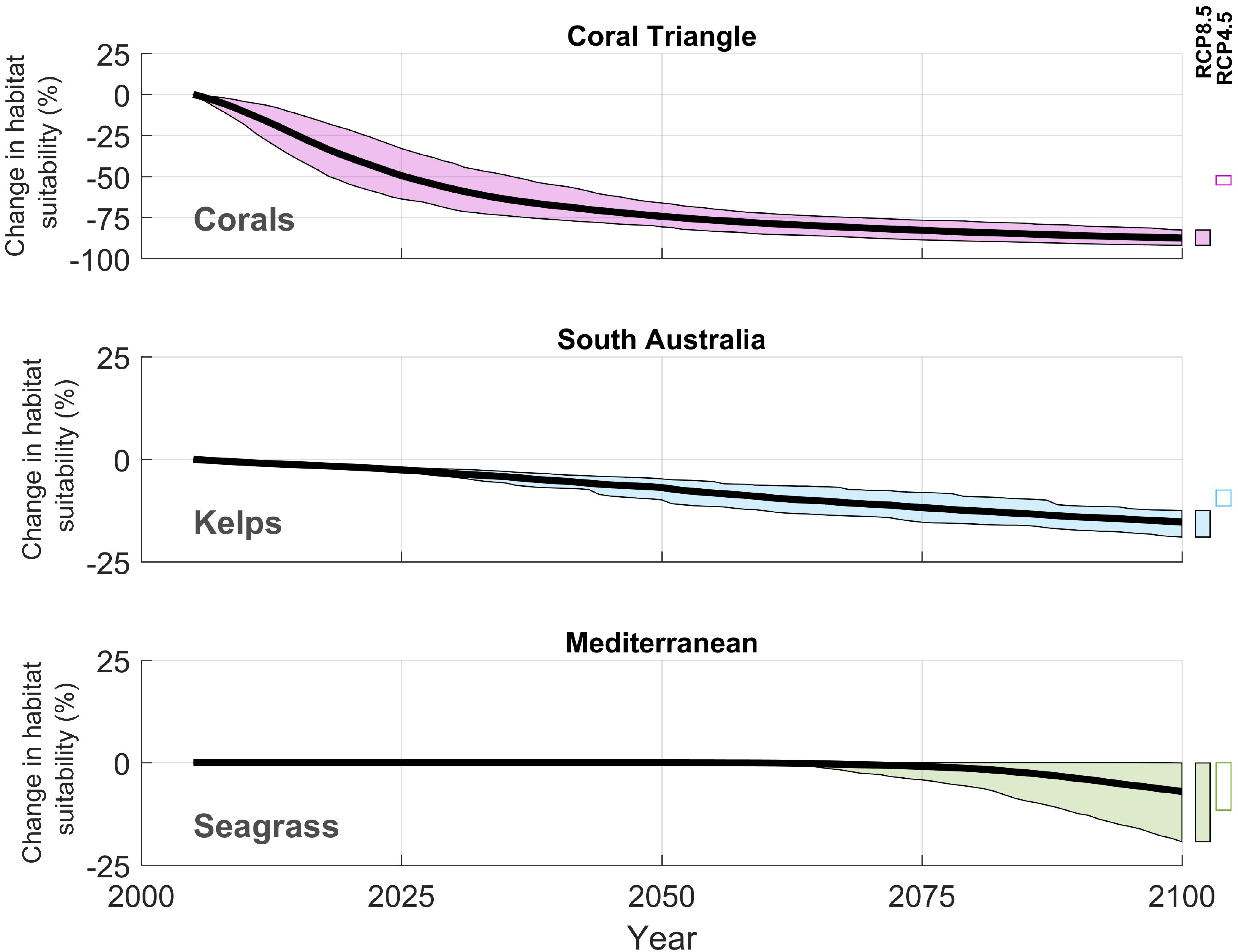
RCP8.5
RCP4.5
Horizontal Isotherm Migration rate (km/yr)
0
2
4
6
8
10
12
14
16
18
20


a
b
c
150
100
50
N° of phytoplankton species
150
100
50
N° of phytoplankton species
100
50
0
Average depth potential
phytoplanktonic community (m)


a
RCP4.5
50
0
-50
Change in potential phytoplanktonic diversity (%)
b
RCP4.5
0
-5
-10
-15
-20
-25
Change in mean depth of potential phytoplanktonic diversity (m)


Corals
Magroalgae
Seagrass
25°N
30°S
90°E
170°E
20°S
45°S
110°E
160°E
48°N
29°N
5°W
43°E
Projected VIM (m/dec)
0
-10
-20
Time to Thermal limit (yrs)
150
75
0
%
years
0.4
0.3
0.2
0.1
0.15
0.05
0
100
200
300
400
500

Corals
Magroalgae
Seagrass
25°N
30°S
90°E
170°E
20°S
45°S
110°E
160°E
48°N
29°N
5°W
43°E
Projected VIM (m/dec)
0
-10
-20
Time to Thermal limit (yrs)
150
75
0
%
years
0.25
0.2
0.15
0.1
0.05
0
100
200
300
400
500
0.08
0.06
0.04
0.02



Coral Triangle
South Australia
Mediterranean
RCP8.5
RCP4.5
Change in habitat suitability (%)
Corals
Kelps
Seagrass
25
0
-25
-50
-75
-100
2000
2025
2050
2075
2100
Year