

# Assessing the time of emergence of global ocean fish biomass using ensemble climate to fish simulations

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## Key Points:

- The Time of Emergence (ToE) of marine ecosystem is investigated for the first time using ensemble climate-to-fish simulations
- Emergence of fish biomass is driven by the concentration of lower trophic levels and modulated by temperature through trophic amplification
- The ToE pattern closely follow the signal-to-noise ratio, which is mostly influenced by the strength of the climate change signal

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**Abstract**

Climate change is anticipated to considerably reduce global marine fish biomass, driving marine ecosystems into unprecedented states with no historical analogues. The Time of Emergence (ToE) marks the pivotal moment when climate conditions (i.e. signal) deviate from pre-industrial norms (i.e. noise). Leveraging ensemble climate-to-fish simulations, this study examines the ToE of epipelagic, migratory and mesopelagic fish biomass, alongside their main environmental drivers, for two contrasted climate-change scenarios.

Globally-averaged biomass signals emerge over the historical period. Epipelagic biomass decline emerges earlier (1950) than mesozooplankton decline (2000) due to a stronger signal in the early 20th century, possibly related to trophic amplification induced by an early-emerging surface warming (1915). Trophic amplification is delayed for mesopelagic biomass due to postponed warming in the mesopelagic zone, resulting in a later emergence (2000). ToE displays strong size class dependence, with medium sizes (20 cm) experiencing delays compared to the largest (1 m) and smallest (1 cm) categories.

Regional signal emergence lags behind the global average, with median ToE estimates of 2029, 2034 and 2033 for epipelagic, mesopelagic and migrant communities, respectively, due to systematically larger local noise compared to global one. These ToEs are also spatially heterogeneous, driven predominantly by the signal pattern, akin to mesozooplankton. Additionally, our findings underscore that mitigation efforts (i.e. transitioning from SSP5-8.5 to SSP1-2.6 scenario) have a potential to curtail emerging ocean surface signals by 40%.

**Plain Language Summary**

Climate change is expected to have a significant impact on global marine fish biomass, leading marine ecosystems into unprecedented states. The Time of Emergence (ToE) is the moment when such a shift occurs. This study investigates the ToE of marine fish biomass is investigated using climate-to-fish simulations. Our results suggest that the emergence of global mean fish biomass occurs in the historical period (before 2020) and is controlled by small-size organisms (mesozooplankton) through food availability. We also show that the ToE strongly is highly dependent on organism size and varies regionally. Furthermore, we demonstrate that implementing mitigation policies significantly reduces the ar-

45 eas in which marine ecosystems emerge, thereby limiting the potential negative impacts  
46 of climate change.

## 47 **1 Introduction**

48 Anthropogenic climate change is expected to significantly impact the abundance  
49 and spatial distribution of pelagic communities of high trophic level organisms (HTL)  
50 (Lefort et al., 2015; Lotze et al., 2019; Tittensor et al., 2021). These impacts on HTLs  
51 arise from a myriad of climate-related stressors encompassing changes in lower trophic  
52 level organisms (LTL, i.e. microzooplankton, mesozooplankton), temperature, oxygen  
53 concentration, pH and ocean currents (Bijma et al., 2013; Bopp et al., 2013). Yet, the  
54 foremost pivotal factors driving these changes remain changes in temperature and pri-  
55 mary production (Pörtner & Peck, 2011; Heneghan et al., 2021). Ocean warming, in par-  
56 ticular, is indeed expected to accelerate metabolic rates and thus energy dissipation. In  
57 addition, temperature changes can affect the food consumption of organisms in differ-  
58 ent ways depending on the available food concentration (Guiet et al., 2016), resulting  
59 in a complex and diverse ecosystem response to temperature changes. In general, these  
60 changes are anticipated to potentially reduce HTL biomass for a given level of primary  
61 production (Heneghan et al., 2019). Moreover, ocean temperature changes is anticipated  
62 to cause a global decline in primary production (Pörtner et al., 2022), notably through  
63 increased stratification, which reduces nutrient concentrations in the euphotic zone. This  
64 will induce a global decline in LTL organisms, which are the fundamental energy source  
65 fuelling marine ecosystems (Chavez et al., 2011), and in turn a marked decrease in fish  
66 biomass. Given the importance of marine resources for both food security and the global  
67 economy, it is imperative to identify when and where these climate-induced impacts will  
68 exceed the natural variations of the marine ecosystems.

69 The Time of Emergence (ToE), as defined by Hawkins and Sutton (2012), repre-  
70 sents the moment when a climate change signal becomes distinguishable from the inher-  
71 ent natural variability. ToE is typically identified when the ratio of anthropogenic sig-  
72 nal (S) to natural climate noise (N), expressed as SNR, permanently exceeds a prede-  
73 termined threshold (as seen in studies such as Giorgi and Bi (2009)). Historically con-  
74 ceived to assess when local climates deviate from their historical norms, ToE analysis  
75 holds particular relevance for ecosystems with limited adaptive capacity (Beaumont et  
76 al., 2011; Deutsch et al., 2008). Originally applied to terrestrial areas (Giorgi & Bi, 2009;

77 Diffenbaugh & Scherer, 2011), this concept has been extended to analyse changes in key  
78 environmental drivers of marine ecosystems, encompassing physical (Ying et al., 2022;  
79 Gopika et al., In prep; Santana-Falcón & Séférian, 2022) and biogeochemical variables  
80 (Keller et al., 2014; Rodgers et al., 2015; Henson et al., 2017). Earth System Model pro-  
81 jections consistently indicate early emergence of sea surface temperature (SST) signals  
82 and much later emergence in primary production (Keller et al., 2014; Rodgers et al., 2015;  
83 Henson et al., 2017; Schlunegger et al., 2020). However, the ToE concept has not yet been  
84 applied to pelagic ecosystems projections.

85 Marine ecosystem models (MEMs) have been pivotal in projecting and understand-  
86 ing the impacts of climate change on marine ecosystems, notably through initiatives such  
87 as the Fisheries and Marine Ecosystem Model Intercomparison Project (FishMIP, Tittensor  
88 et al. (2018); Lotze et al. (2019); Tittensor et al. (2021)). On average, these projections  
89 indicate a reduction in global fish biomass at the end of the century of around 15-20%  
90 in a high emissions scenario (SSP5-8.5), and of around 5-7% in a low emissions scenario  
91 (SSP1-2.6) Lotze et al. (2019); Tittensor et al. (2021)). In addition, these studies high-  
92 light a spatial heterogeneity in the fish biomass response to climate change, hitting at  
93 potential increases in the Arctic Ocean and South Polar region while predicting decline  
94 elsewhere.

95 The primary objective of this study is to implement the ToE concept within pro-  
96 jections generated by a global-scale marine ecosystem model, examining and contrast-  
97 ing these ToE with the pivotal environmental variables driving this model. Using the mech-  
98 anistic ecosystem model APECOSM forced by ensemble simulations from the IPSL-CM6A-  
99 LR Earth System Model, for two contrasted emission scenarios(SSP5-8.5 and SSP1-2.6),  
100 we will first show that, when considering global average, the ToE is very early for the  
101 epipelagic (1950) and slightly later for the migratory and mesopelagic fish biomass (around  
102 2000), with a strong dependency to the size class considered. Next, we show that the ToE  
103 at regional scale is considerably later than the globally averaged one, with strong depen-  
104 dency to the region and community considered. The paper is structured as follows. Sec-  
105 tion 2 describes the ecosystem and climate models, the simulation protocol and the method-  
106 ology used to calculate the ToEs. Section 3 compares the ToEs estimated for the main  
107 ecosystem drivers, namely ocean temperature and mesozooplankton concentration, with  
108 those estimated for fish biomass. Summary and discussion are provided in 4.

## 2 Data and method

### 2.1 Marine ecosystem model

This study uses the Apex Predators ECOSystem Model (APECOSM, Maury et al. (2007); Maury (2010)) to simulate changes in marine fish biomass in the global ocean. APECOSM is a Eulerian ecosystem model that mechanistically represents the three-dimensional dynamics of size-structured pelagic populations and communities. It integrates individual, population and community levels and includes the effects of life-history diversity with a trait-based approach (Maury & Poggiale, 2013). Energy uptake and use for individual growth, development, reproduction, somatic and maturity maintenance are modelled according to the Dynamic Energy Budget (DEB) theory (Koojman, 2010), with metabolic rates dependent on both food and temperature.

APECOSM also includes important ecological processes such as opportunistic size-structured trophic interactions and competition for food, predatory, disease, ageing and starvation mortality, key physiological aspects such as vision and respiration, as well as essential processes such as three-dimensional passive transport by marine currents and active habitat-based movements (Faugeras & Maury, 2005), schooling and swarming (see Maury et al. (2007); Maury and Poggiale (2013); Maury (2017)).

In this study, we used the same APECOSM configuration as in Barrier et al. (2023), in which the model was used to analyse the ENSO-related variability of the biomass of epipelagic fish in the tropical Pacific Ocean. Three generic communities are simulated:

- The epipelagic community, which includes the organisms inhabiting surface waters during both day and night. Its vertical distribution is influenced by light and visible food during the day as well as temperature and oxygen during both day and night, while its functional response to prey is influenced by light and temperature.
- The migratory mesopelagic community, which includes organisms that feed at night in the surface layer and move to deeper waters during the day. Its vertical distribution is influenced by light during both day and night and visible food during the night.

- 138 • The resident mesopelagic community, which includes organisms that remain at depth  
139 during both day and night. Its vertical distribution is influenced by light and vis-  
140 ible food during the day.

141 A more detailed description of this 3 community configuration is provided in (Barrier  
142 et al., 2023), in addition to a more thorough description of the model.

## 143 2.2 Climate model

144 In this study, APECOSM is forced by 3D physical (temperature, ocean currents)  
145 and biogeochemical (diatoms, microzooplankton, mesozooplankton, organic detritus, oxy-  
146 gen, light) outputs of the IPSL-CM6A-LR Boucher et al. (2020) Earth System Model  
147 (ESM). This ESM has recently been used by the Fisheries and Marine Ecosystem Model  
148 Intercomparison Project (FishMIP) to assess the impacts of climate change on marine  
149 ecosystems, e.g. (Tittensor et al., 2021).

## 150 2.3 APECOSM Simulation protocol

151 The APECOSM simulation protocol used in this study is in agreement with the  
152 CMIP6 standards (Eyring et al., 2016). We therefore employ the same naming conven-  
153 tions.

154 First, a 100-year spin-up simulation has been performed using the outputs of the  
155 *piControl-spinup* ESM simulation, starting from a uniform biomass distribution of  $1^{-34} J.m^{-2}.kg^{-1}$   
156 for each community and size class. The end of the spin-up simulation is then used as a  
157 restart to run a pre-industrial simulation, using the outputs from the *piControl* climate  
158 simulation. The latter simulation was integrated for 500 years (1850-2349). Preindus-  
159 trial  $CO_2$  concentrations are prescribed in both the *piControl-spinup* and *piControl* cli-  
160 mate simulations.

161 Next, 6 members of the *historical* simulations have been run using specific years  
162 of the *piControl* simulation as initial state. These years are chosen to ensure consistency  
163 with the climate simulations. The *historical* climate simulations cover the period from  
164 1850 to 2014 and are constrained by observed annual greenhouse gas emissions. Finally,  
165 the end of the 6 *historical* simulation members have been used as initial states for the  
166 corresponding climate change simulations under the SSP5-8.5 and SSP1-2.6 "Shared So-

Simulation	Initial conditions	Simulation period
<i>piControl-spinup</i>	Uniform biomass distribution	1750-1850
<i>piControl</i>	<i>piControl-spinup</i>	1850-2349
<i>hist-r1</i>	<i>piControl</i> (1909-12-31)	1850-2014
<i>hist-r2</i>	<i>piControl</i> (1869-12-31)	1850-2014
<i>hist-r3</i>	<i>piControl</i> (1929-12-31)	1850-2014
<i>hist-r4</i>	<i>piControl</i> (1949-12-31)	1850-2014
<i>hist-r6</i>	<i>piControl</i> (2029-12-31)	1850-2014
<i>hist-r14</i>	<i>piControl</i> (1969-12-31)	1850-2014
<i>ssp-r1</i>	<i>hist-r1</i>	2015-2100
<i>ssp-r2</i>	<i>hist-r2</i>	2015-2100
<i>ssp-r3</i>	<i>hist-r3</i>	2015-2100
<i>ssp-r4</i>	<i>hist-r4</i>	2015-2100
<i>ssp-r6</i>	<i>hist-r6</i>	2015-2100
<i>ssp-r14</i>	<i>hist-r14</i>	2015-2100

**Table 1.** Simulations performed with the APECOSM model. The middle column indicates the initial condition used. If no date is provided, the end of the simulation is used.

167 socioeconomic Pathways” scenarios. These two scenarios represent the upper and lower ends  
 168 of the CMIP6 future forcing pathways in the Integrated Assessment Modeling literature.  
 169 SSP5-8.5 updates the CMIP5 RCP8.5 pathway and is the only SSP scenario with emis-  
 170 sions high enough to produce a radiative forcing of  $8.5 \text{ W.m}^{-2}$  in 2100 (O’Neill et al.,  
 171 2016). SSP1-2.6 updates the CMIP5 RCP2.6 pathway and is anticipated to produce a  
 172 multi-model mean of significantly less than  $2^\circ\text{C}$  warming by 2100 (O’Neill et al., 2016).

173 All the simulations are summarised in Table 1. It should be noted that the lim-  
 174 ited number of members used in this study is constrained by the availability of the bio-  
 175 geochemical variables in the IPSL-CM6-LR climate change scenarios.

## 176 2.4 Time of Emergence

177 As discussed in the introduction, ToE typically marks the moment when the ra-  
 178 tio of anthropogenic signal (S) to natural climate noise (N), SNR, permanently exceeds

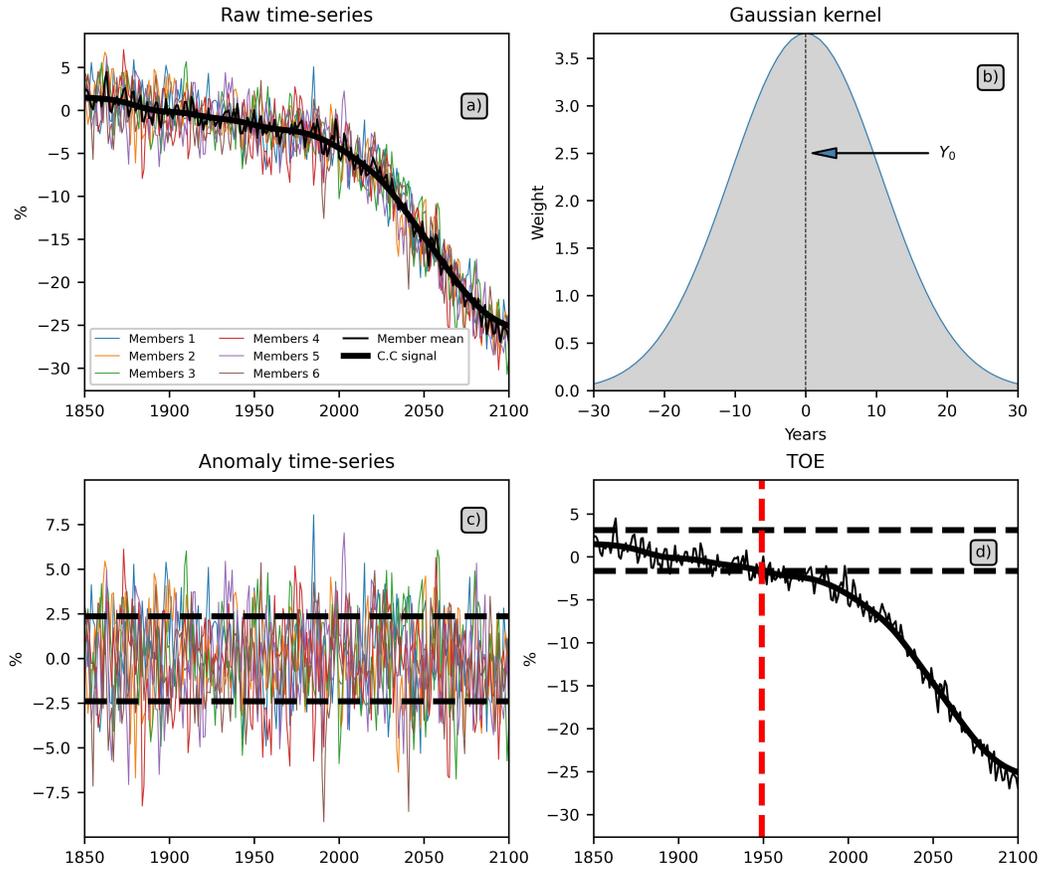
179 a predefined threshold (Giorgi & Bi, 2009). In this section, we illustrate the presenta-  
180 tion of the methodology used to calculate the signal  $S$ , the noise  $N$  and the ToE using  
181 time series of global mean epipelagic fish biomass.

182 The methodology employed in (Hawkins & Sutton, 2012) for signal estimation, which  
183 assumes a proportional scaling between local changes and global variations, cannot be  
184 applied in our context. While this assumption holds true at first order for SST, it does  
185 not hold for biogeochemical and biological variables, whose climate change signal shows  
186 strong spatial and temporal heterogeneity (Lotze et al., 2019; Tittensor et al., 2021). Rather,  
187 the climate change signal in our approach is derived by averaging the historical and sce-  
188 nario time series over the 6 members, as shown in Fig. 1a (thin black curve). Since these  
189 members share identical external forcings and differ only in their initial state, the multi-  
190 member average serves as a good first approximation of the climate change signal. How-  
191 ever, residual noise persists due to the limited number of available members. To remove  
192 this noise, a Gaussian filter with a standard deviation of 15 years is applied to smooth  
193 the multi-member mean (Fig. 1b). The resulting smoothed time series (thick black curve  
194 in Fig. 1a) is regarded as the climate change signal  $S$ .

195 Natural variability is then estimated by removing this climate change signal from  
196 each member time series. The resulting time series (Fig. 1c) represent the anomalies in  
197 fish biomass due solely to high-frequency climate and ecosystem variability. The noise  
198  $N$  is then estimated by calculating the standard deviation of the anomalies over the time  
199 and member dimensions (black dashed curve in Fig. 1c).

200 Finally, we define ToE as the year when the climate change signal permanently ex-  
201 ceeds the envelope of natural variability (black dashed curve in Fig. 1d), which we de-  
202 fine as the historical multi-member mean computed between 1850 and 1900 plus or mi-  
203 nus the standard deviation of the anomalies ( $N$ , Fig. 1d). To avoid potential artefacts  
204 due to truncation of the Gaussian smoothing kernel used to extract the signal, we con-  
205 sider that there is no emergence if the estimated ToE is later than 2085.

206 ToEs are calculated both globally and at each grid cell for temperature at the sur-  
207 face and averaged between 500 and 1000 m, surface mesozooplankton concentrations, and  
208 for the vertically integrated fish biomass density of each community and each size class.  
209 In addition, total fish biomass (i.e. biomass integrated over the entire size range) is also  
210 evaluated for each community.



**Figure 1.** Overview of steps for calculating the time of emergence. Displayed is the time series for global mean epipelagic fish biomass. (a) Single-member time series (coloured lines), multi-member mean (thin black line) and climate change signal (thick black line). (b) Gaussian kernel illustration used to smooth the multi-member mean. (c) Computed noise obtained by subtracting the climate change signal from the original time series. These anomalies represent the range of natural variability (dashed lines). (d) Calculation of the time of emergence (dashed red line) as the moment when the climate change signal is permanently outside the range of natural variability.

## 3 Results

In this section, we first discuss the ToE for global mean temperature at the surface and between 500-1000 m, surface mesozooplankton concentrations and global mean total biomass for each community. Next, we investigate the ToE of mean fish biomass as a function of size. Finally, ToE computed from global mean time series is compared to the ToE computed on regional scales and the spatial patterns of ToE are described.

### 3.1 Global mean ToE

#### 3.1.1 *Environmental drivers and total fish biomass*

Fig. 2 shows the global mean anomalies of temperature at the surface (SST) and averaged between 500 and 1000 m, surface mesozooplankton concentrations and fish biomass density (integrated between 0-1000m) of each community relative to the 1850-1900 period. The global mean SST starts increasing from 1900. This warming notably accelerates from 2000 onwards in the SSP5-8.5 scenario (red curve), exceeding  $3.5^\circ$  by the end of the 21st century (Fig. 2a) with respect to pre-industrial conditions. Conversely, in the SSP1-2.6 scenario, the warming reaches a plateau from the middle of the century (around  $1.5^\circ$ ). Because of minimal noise attributable to the global average, SST emerges very early (1915) in both scenarios. The warming between 500 and 1000 m is weaker than that of the SST and starts later, resulting in a delayed emergence (around 1945).

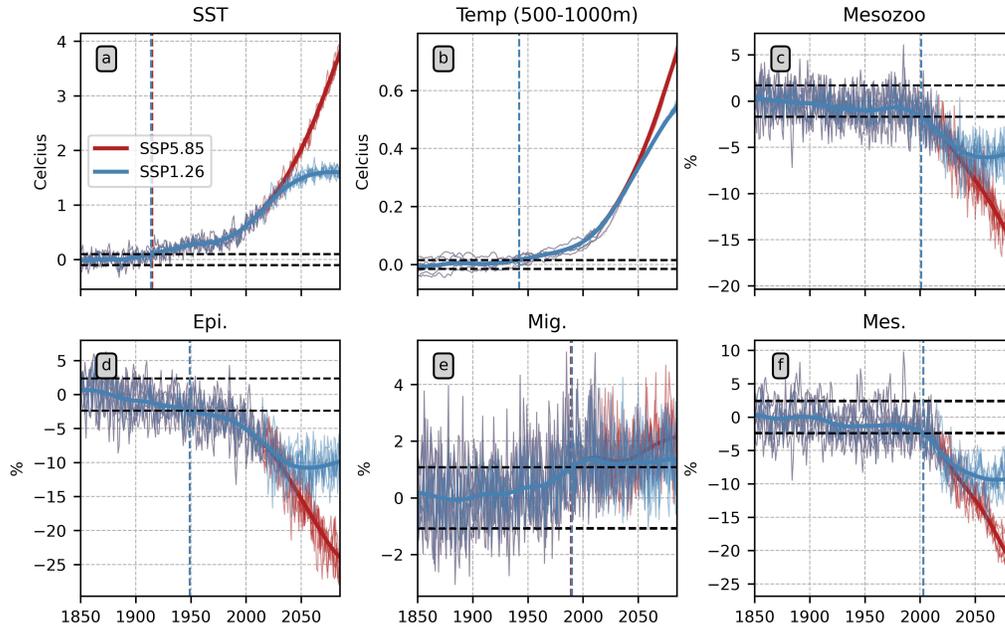
Global surface mesozooplankton anomalies exhibit a strikingly similar low-frequency evolution in both scenarios (Fig. 2c), opposing that of temperature anomalies. They indeed show a pronounced decline starting at the turn of the 21st century. This reduction persists almost linearly until the century's end for the SSP5-8.5 scenario, reaching -15%. Conversely, in the SSP1-2.6 scenario, this decline moderates, with a relative decrease plateauing at -5% by the mid-century mark in 2050. Because of a weaker signal-to-noise ratio compared to temperature, the climate change signal for mesozooplankton emerges later (2001) compared to SST (1915).

Epipelagic fish biomass evolution mirrors that of mesozooplankton, suggesting a bottom-up control mechanism. However, by the end of the 21st century, the relative decline in epipelagic biomass surpasses that of mesozooplankton for both the SSP5-8.5 and SSP1-2.6 scenario, with reductions of 25% and 10% respectively for epipelagic biomass

241 compared to -15% and -5% for mesozooplankton. This heightened decline in epipelagic  
242 biomass is likely linked to trophic amplification, potentially driven by warmer temper-  
243 atures, as discussed in de Luzinai et al. (2023). Furthermore, the epipelagic decline out-  
244 paces that of mesozooplankton throughout the 20th century, presumably for the same  
245 reason. This trophic amplification leads to an early emergence of global mean epipelagic  
246 biomass (1949).

247 Mesopelagic biomass evolution closely follows that of epipelagic biomass in terms  
248 of both timing and amplitude. Despite exhibiting a larger relative amplitude, it also mir-  
249 rors the evolution of mesozooplankton and detritus concentrations (not shown), their pri-  
250 mary food source, further suggesting a bottom-up control mechanism likely intensified  
251 by trophic amplification. However, although the relative noise of global mesopelagic and  
252 epipelagic biomass is similar (around 2%), the former declines more slowly than the lat-  
253 ter, which results in a later emergence of mesopelagic fish (2001). This milder decrease  
254 could be attributed to a weaker trophic amplification during the early stages of the in-  
255 dustrial era. Initially, the warming primarily affects the surface and gradually penetrates  
256 in deeper layers, resulting in a delayed warming effect in the mesopelagic zone and con-  
257 sequently in a less pronounced trophic amplification during the initial period. The trophic  
258 amplification gradually intensifies as surface warming signals penetrate deeper into the  
259 ocean over time (Fig. 2a and b).

260 In comparison to epipelagic and mesopelagic communities, global biomass changes  
261 of the migratory community is considerably weaker in 2100, increasing of +2% in the  
262 SSP5-8.5 scenario and 1% in the SSP1-2.6 scenario. Identifying a plausible mechanism  
263 driving these changes is more challenging than for the other communities, as the evo-  
264 lution of migratory biomass does not align with any of the predominant environmental  
265 drivers. Nonetheless, these changes emerge around the same time frame (1990) than those  
266 simulated for the mesopelagic community (2001), primarily because the weaker noise in  
267 the migratory (N of 1.07%) compared to the mesopelagic community (N of 2.35%) com-  
268 pensates for the weaker signal simulated at the turn of the 20th century (S of 2.32% and  
269 -25.56%, respectively).



**Figure 2.** Global mean anomalies of temperature at the surface (a) and averaged between 500 and 1000 m (b), relative surface mesozooplankton concentrations (c) and global mean fish biomass for the epipelagic, migratory and mesopelagic communities (d-e-f). The thin lines represent the individual members, and the thick lines represent the climate change signal.

### 3.1.2 Sensitivity to the size class

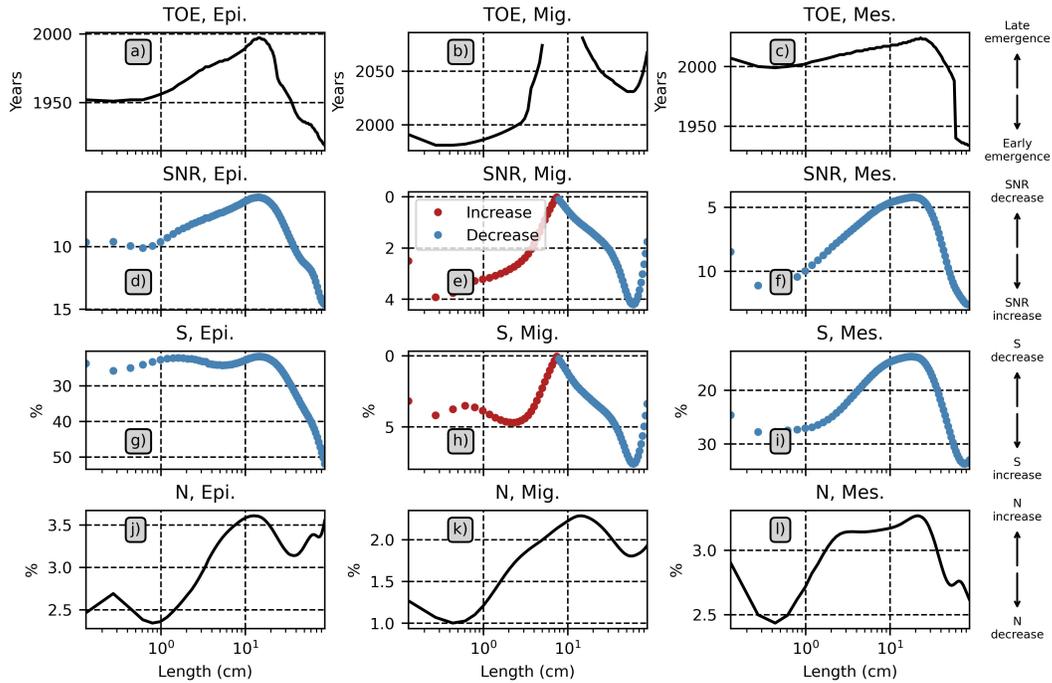
As discussed for example in (Barrier et al., 2023), the response of marine fish biomass to changes in environmental drivers is size dependent. Consequently, the natural variability  $N$ , the climate change signal  $S$  and, hence, the ToE of fish biomass are expected to vary with size.

Fig. 3 allows examining the ToE sensitivity to the organisms size class for each community and the primary factor governing this sensitivity, whether it is noise or signal. We present only the results for the SSP5-8.5 scenario as they are insensitive to the scenario considered. The upper panels show the ToE as a function of size for each community, while lower panels illustrate the signal-to-noise ratio (SNR), the relative signal ( $S$ ) and the relative noise ( $N$ ). The ToE is early (1950) and stable for size classes smaller than 1 cm (Fig. 3a) and then increases from 1950 to 2000 for sizes ranging from 1 cm to 15 cm. This increase can be directly related to an increase in the noise within this size range (Fig. 3j), resulting in a weaker SNR (Fig. 3d) and therefore a delayed emergence. For

284 sizes exceeding 15 cm, the ToE experiences a steep decline, with the largest organisms  
 285 (1 m) reaching an emergence date of 1920. This decline can predominantly be attributed  
 286 to a signal increase within this size range (Fig. 3g).

287 The ToE for the mesopelagic varies with size in a similar way to the epipelagic com-  
 288 munity, reaching a maximum near 25 cm, albeit for different reasons. For the mesopelagic  
 289 community, the SNR (Fig. 3f), and consequently the ToE (Fig. 3c), are primarily driven  
 290 by the signal (Fig. 3i), which decreases up to 25 cm and then increases.

291 In contrast to epipelagic and mesopelagic communities, the signal of the migratory  
 292 community (Fig. 3b) does not emerge for all size classes, with no signal emerging be-  
 293 tween 5 and 15 cm. This absence of emergence for intermediate size classes is attributed  
 294 to a change in signal sign for 10 cm organisms (Fig. 3e), leading to a negligible SNR around  
 295 this size class. In addition, the noise increase also contributes to the ToE increase for  
 296 sizes smaller than 20 cm 3h).



**Figure 3.** Time of emergence (a-c), signal to noise (d-f) ratio, relative signal (g-i) and relative noise (j-l) for epipelagic (left), migratory (middle) and mesopelagic (right) communities. In the second and third rows, biomass increase and decrease are depicted by red and blue dots, respectively. The y-axis are ordered in a way to facilitate the interpretation of the results.

## 3.2 Regional ToE

### 3.2.1 Comparison with global mean ToE

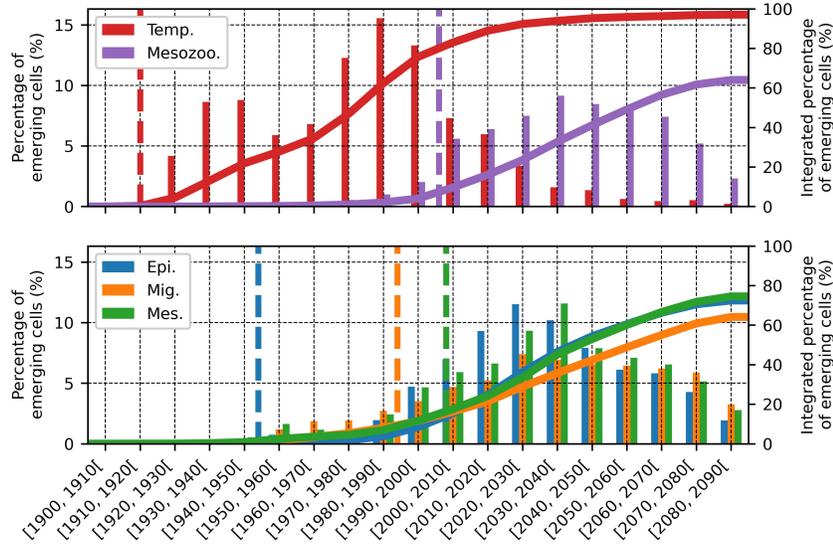
The previous subsection demonstrates that, when globally averaged, fish biomass signals emerge early, mostly during the historical period. This result is likely to be related to a significant reduction in noise through spatial averaging, leading to an increase in SNR. In this subsection, the ToE calculated at regional scale (at grid scale) is compared to the ToE of global mean time series. As the findings remain consistent across the two scenarios considered, we focus on the SSP5-8.5 scenario.

Fig. 4 shows the percentage of the ocean surface where a signal emerges each decade (vertical bars) alongside the cumulative surface where a signal has emerged over time (continuous line). Regional SSTs exhibit early regional emergence, starting between 1920 and 1930 and peaking between 1970 and 1990. In terms of cumulative percentage, SST signals have emerged over about 90% of the ocean surface by 2020, reaching 97% by the end of the century. In contrast, regional mesozooplankton biomass start emerging much later, around 1970, and peak in 2030. By 2020, mesozooplankton has emerged over only 23% of the ocean surface, gradually increasing to 64% by the end of the century. This corresponds to a time lag of approximately 50 years between the regional ToE for mesozooplankton and SST.

The timing of regional emergence for total fish biomass is comparable for all three communities, with the mesopelagic and migratory communities emerging slightly before the epipelagic community. Consequently, the percentages of the ocean surface showing emergence are qualitatively similar between communities, ranging from 28% to 36% by 2020 and 64 to 75% by 2100. The timing of emergence for regional fish biomass is similar to that of mesozooplankton (purple curve) but about a decade earlier, especially for epipelagic organisms, confirming both the bottom-up influence of lower trophic levels on higher trophic levels and the trophic amplification phenomenon already discussed for global scale (Fig. 2).

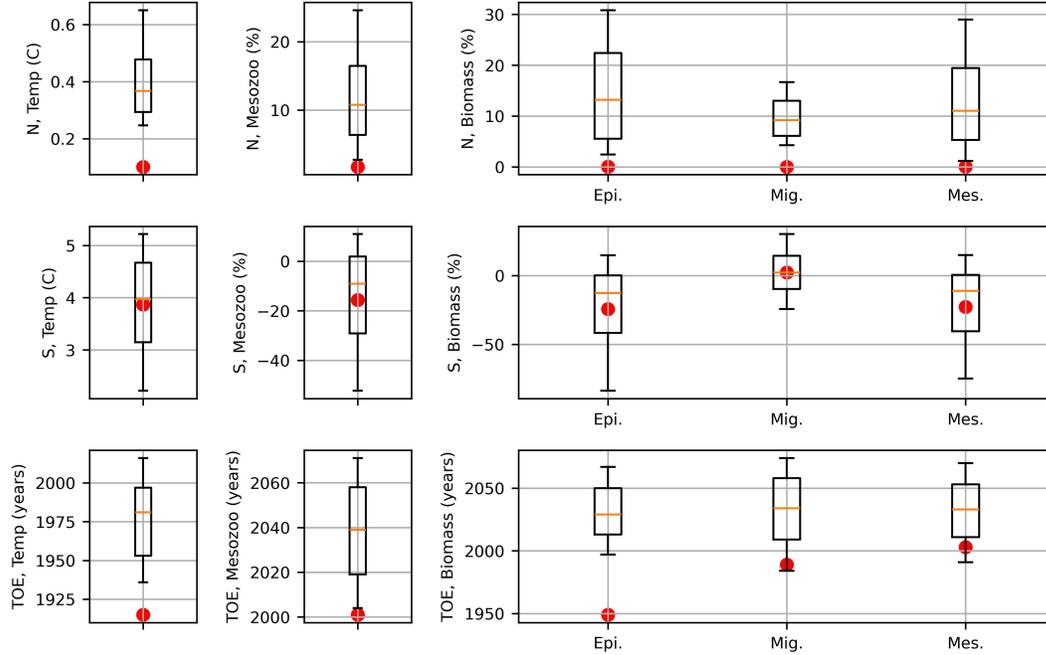
For all variables considered here, the peaks of regional emergence occur later than the emergence of the global mean time series. For example, the peak of regional SST emergence occurs 60 years later than the emergence of the global mean SST, while the lag

327 is of about 30 years for mesozooplankton, 75 years for epipelagic and 35 years for mi-  
 328 gratory and mesopelagic fish communities (dashed lines in Fig. 4).



**Figure 4.** Percentage of the ocean surface where a signal has emerged at grid scale during a given decade (x-axis) for SST (red bars) mesozooplankton concentration at the surface (purple bars), biomass of the epipelagic fish community (blue), mesopelagic migratory fish community (orange), mesopelagic resident fish community (green). The continuous lines show the corresponding cumulative percentages. The dashed vertical lines indicate the ToE of global mean time-series.

329 Fig. 5 compares the  $10^{th}$ ,  $25^{th}$ ,  $50^{th}$  (median),  $75^{th}$  and  $90^{th}$  percentiles of the lo-  
 330 cal noise  $N$  (upper panels), signal  $S$  (middle panels) and ToE (lower panels) distributions  
 331 with the values obtained from the global mean time series (red dots). In all cases, the  
 332 noise values for global averages are either smaller or close to the  $10^{th}$  percentile of the  
 333 local noise. Conversely, the global mean signal aligns more closely to the signal calcu-  
 334 lated locally, falling between the  $25^{th}$  and  $75^{th}$  percentiles for all variables. Consequently,  
 335 due to this considerably weaker noise and relatively consistent signal at global scale, global  
 336 ToE precedes that of local ones. For example, the ToE for global mean SST, mesozoo-  
 337 plankton and epipelagic fish biomass lies below the  $10^{th}$  percentile of the local ToE, while  
 338 it ranges between the  $10^{th}$  and the  $25^{th}$  percentiles for migratory and mesopelagic fish  
 339 biomass.



**Figure 5.** Whisker plot showing the 10<sup>th</sup>, 25<sup>th</sup>, 50<sup>th</sup>, 75<sup>th</sup> and 90<sup>th</sup> percentiles of spatial noise, signal and time of emergence for sea surface temperature, surface mesozooplankton and fish biomass. Red dots indicate the values obtained from the global time series. Mesozooplankton and fish biomass noise and signal are represented in anomalies relative to the historical (1850-1950) global mean value.

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### 3.2.2 *Spatial patterns*

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In the following, the spatial patterns of ToE for SST, surface mesozooplankton and total fish biomass per community are analysed. The focus is laid on the SSP5-8.5 scenario, where over 60% of the ocean surface exhibits emergence at the end of the century for all biological variables.

345

#### **Sea surface temperature**

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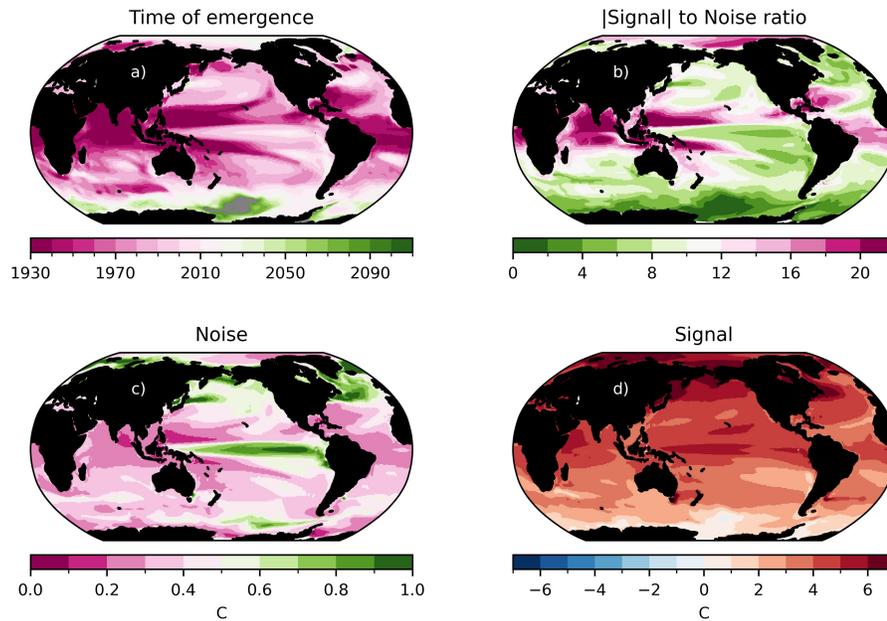
Fig. 6a shows the ToE map for SST. As expected from Fig. 4, most of the oceanic regions emerge early. In particular, the earliest emergence occurs in the tropical Indian Ocean, the tropical Atlantic and the Western Pacific. However, several areas exhibit a late emergence, such as the eastern equatorial Pacific, which manifests emergence around 2010, along with mid-latitude regions and Antarctica. These patterns are consistent with

351 findings from previous studies derived from other ESMs (see for instance Fig. 4 of Schlunegger  
352 et al. (2020)).

353 Fig. 6b shows the SNR map for SST, which is closely related to ToE. Here, the noise  
354 (Fig. 6c) is defined as the standard deviation of the anomalies relative to the climate change  
355 signal (see section 2.4), and the signal (Fig 6d) is defined as the difference between the  
356 SSP5-8.5 multi-member mean SST averaged between 2070 and 2100 and the historical  
357 multi-member SST averaged between 1850 and 1900. The SNR pattern mirrors the ToE  
358 map, indicating an early emergence in regions with a large SNR ratio and a late emer-  
359 gence in areas with a smaller ratio. The SST signal (Fig. 6d) shows much less spatial  
360 variation than the noise (Fig. 6c) and the SNR is predominantly influenced by the noise,  
361 with a spatial correlation between the SNR and the inverse of the noise reaching 0.71.  
362 In particular, the large noise and hence the late emergence of SST in the tropical Pa-  
363 cific are related to the strong ENSO variability (Diaz et al., 2001). Similarly, in the North  
364 Pacific and the Atlantic oceans, delayed emergence arises from the large noise induced  
365 by the Pacific North American pattern and the North Atlantic Oscillation (Hurrell &  
366 Deser, 2009), respectively. The correlation of SNR with the signal is 0.47. In particu-  
367 lar, the weak SNR and hence the late emergence of SST in the Southern Ocean is due  
368 to a weaker signal.

### 369 **Surface mesozooplankton**

370 As expected from Fig. 4, the ToE map for mesozooplankton shows broad regions  
371 where the signal has not emerged by the end of the century. Signals have emerged in most  
372 of the tropical ocean, with early emergence occurring in the equatorial Atlantic, west-  
373 ern Pacific and western Indian Ocean. On the contrary, ToE patterns are more patchy  
374 and less homogeneous at mid and high latitudes, with early emergence in the subtrop-  
375 ical Pacific gyres (2010) and no emergence on their flanks. Compared to the SST, the  
376 mesozooplankton signal displays very large spatial variations, from a strong decrease in  
377 the tropics, especially in the equatorial Atlantic and western Pacific, to a strong increase  
378 in the subtropical Pacific gyres. These regions with a prominent mesozooplankton re-  
379 sponse generally correspond to those with early emergence. In contrast to SST, the signal-  
380 to-noise ratio and hence the ToE for mesozooplankton is predominantly driven by the  
381 signal (spatial correlation of 0.59) rather than by the noise (spatial correlation with the  
382 inverse of the noise of -0.02). This is particularly true in regions where the signal-to-noise

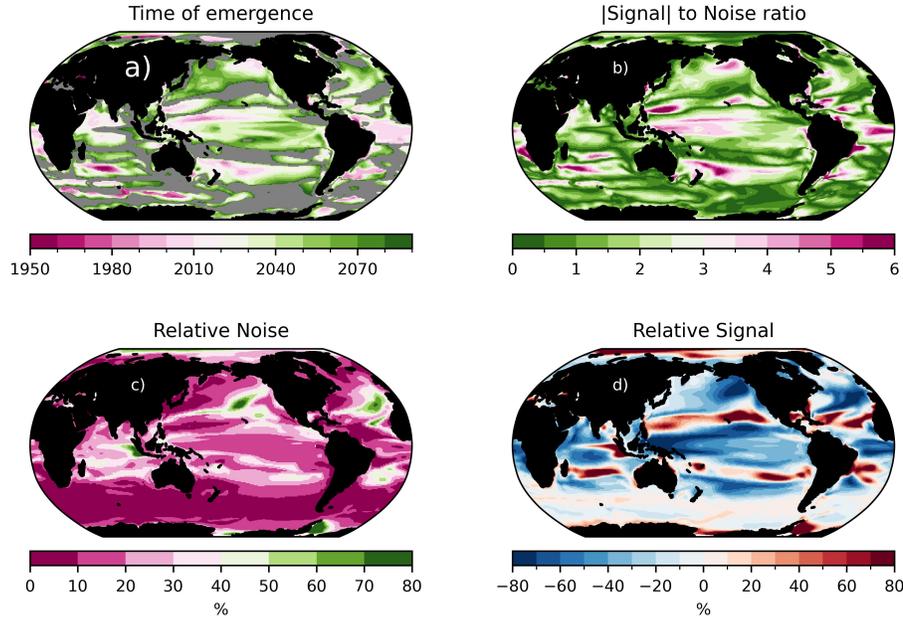


**Figure 6.** Maps of ToE (a), SNR (b), noise (c) and signal (d) for SST. Noise is calculated as the standard deviation of the anomalies relative to the climate change signal. Signal is calculated as the difference between the SSP585 temperature averaged over the 2070-2100 period and the historical temperature averaged between 1850 and 1900. In a), grey shadings indicate areas that have not emerged.

383 ratio is the highest (pink areas in Fig. 7b), which are associated with very strong sig-  
 384 nals (either positive or negative). These regions are also the earliest to emerge (before  
 385 2010).

### 386 **Fish biomass**

387 The SNR, and consequently the associated ToE, predominantly mirror the signal  
 388 within the three communities, as illustrated in Fig. 8e, f and g. Areas exhibiting early  
 389 emergence coincide with those displaying stronger signal, whether positive or negative.  
 390 This visual assessment finds further support in the pattern correlation between the SNR  
 391 and the relative signal, which reaches 0.76, 0.74 and 0.89 for the epipelagic, migratory  
 392 and mesopelagic communities, respectively. Conversely, the correlation with the inverse  
 393 of the relative noise is much lower (0.04, -0.06 and -0.004, respectively).



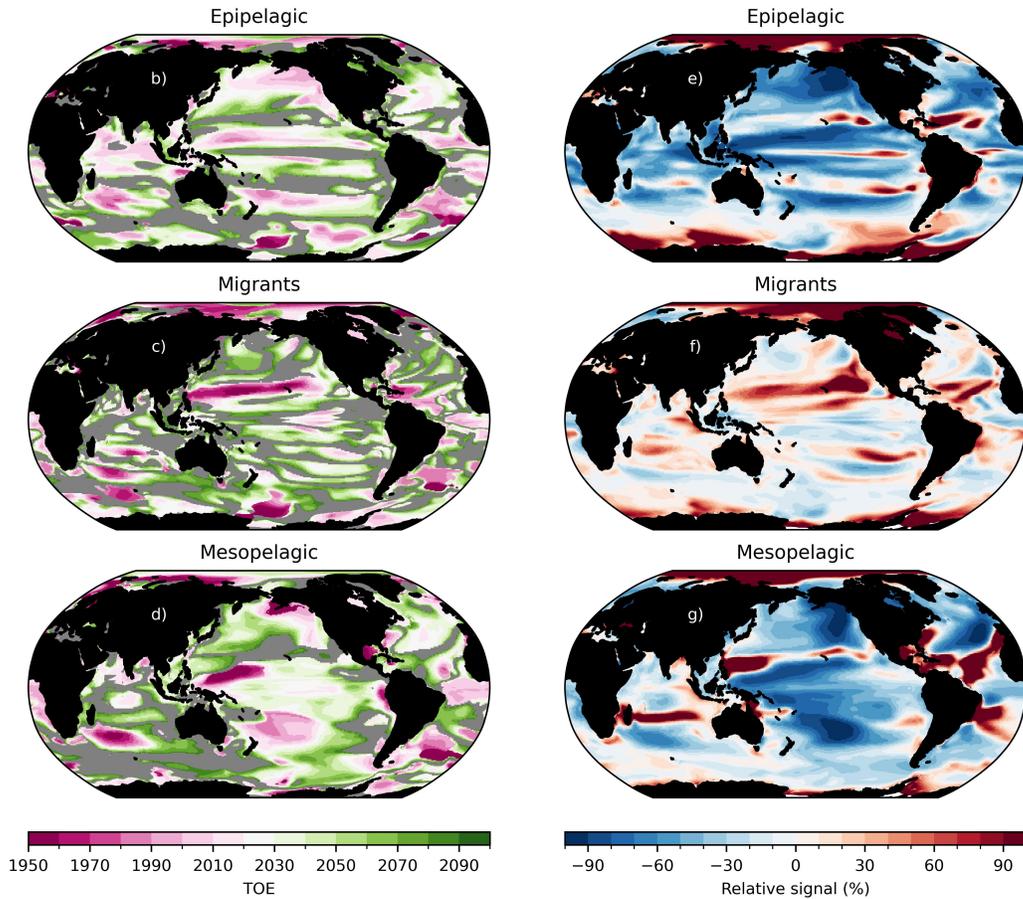
**Figure 7.** Time of emergence (a), signal-to-noise ratio (b), noise (c) and signal (d) for sea surface mesozooplankton concentration. The noise is given as the standard deviation of the anomalies relative to the climate change signal. The signal is provided as the difference between the SSP5-8.5 mesozooplankton averaged over the 2070-2100 period and the historical mesozooplankton averaged between 1850 and 1900. The latter is also used to normalise the standard deviation and signal, which are presented as percentages. In a), grey shading indicates areas that have not emerged.

394 Although the three communities display a similar emergence timeline at the global  
 395 scale (Fig. 8a), the spatial patterns of their ToE show striking disparities, as illustrated  
 396 in Fig. 8b-d. The epipelagic and resident communities emerge over wide regions (Fig.  
 397 8b,d), in contrast to the migratory community, which displays a more fragmented emer-  
 398 gence pattern (Fig. 8c). This distinctive characteristics may be attributed to differences  
 399 in the strength of signal among these communities. Both the epipelagic and mesopelagic  
 400 communities (Fig. 8e,g) display a decline in fish biomass across most oceanic regions,  
 401 which explains the strong decrease of global mean biomass (about -20%, Fig. 2d and f).  
 402 On the other hand, the migratory community exhibits both increasing and decreasing  
 403 signals at a regional scale (Fig. 8f), which explains the small increase (about +2%) of  
 404 global mean migratory fish biomass (Fig. 2e).

405 The epipelagic fish biomass emerges before 2020 in various regions such as the trop-  
406 ical Pacific and Atlantic on both sides of the equator, the northern and southern Pacific  
407 and Atlantic Oceans and southeast of Madagascar (Fig. 8b). These regions of early emer-  
408 gence align with the early emergence of mesozooplankton biomass (Fig. 7a), which cor-  
409 responds to a pronounced decline in mesozooplankton concentration (Fig. 7e) and epipelagic  
410 fish biomass (Fig. 7d). The projected patterns for the epipelagic community resemble  
411 those for mesozooplankton (pattern correlation of 0.61), indicating that changes in meso-  
412 zooplankton concentration are the predominant drivers of projected changes in epipelagic  
413 fish biomass, as already inferred from global mean time series (Fig. 2). This influence  
414 is more substantial than that of temperature, which exhibits a much earlier emergence  
415 and distinctly different patterns (Fig 6d, pattern correlation of -0.00). Although not struc-  
416 turing the ToE spatial patterns for the epipelagic community, warmer temperatures likely  
417 induce early emergence (median value around 2025, Fig. 5), presumably through trophic  
418 amplification (de Luzinai et al., 2023).

419 Regarding the migratory community, the most striking feature is the very early emer-  
420 gence (around 1950) that occurs in the central Pacific, at about 15°N. This area of early  
421 emergence coincides with a strong positive mesozooplankton concentrations signal in the  
422 gyres (Fig. 7d), which in turn leads to a marked increase in the migratory fish biomass  
423 (Fig. 7f).

424 The mesopelagic community shows an emerging signal across extensive regions of  
425 the Pacific and Atlantic Oceans, particularly in areas characterised by moderate to pro-  
426 nounced mesopelagic biomass decline. Signals emerge before 2020 in specific areas, such  
427 as the north of the equatorial western Pacific, off New Zealand and around the Fiji Is-  
428 lands, as well as in the equatorial and South-West Atlantic and the south-western re-  
429 gion of the Indian Ocean off the island of Madagascar. The projected patterns for the  
430 mesopelagic community (Fig. 8c) also demonstrate some resemblance to those of meso-  
431 zooplankton (Fig. 7d, pattern correlation of 0.48), although to a lesser extent compared  
432 to the congruence observed in the epipelagic community. This discrepancy is likely re-  
433 lated to the model representation, where mesopelagic organisms feed on the migratory  
434 community that inhabits mesopelagic waters during the day and on organic detritus, both  
435 of which exhibiting different horizontal distributions than mesozooplankton.



**Figure 8.** (a) Surface of the ocean in which the epipelagic, migratory and mesopelagic total fish biomass emerge in a given decade. The continuous lines show the cumulated percentage. The red and purple lines show the cumulative percentage for temperature and mesozooplankton (cf. Fig 4). (b-c-d) ToE maps for each of the three communities, with non emerging areas in gray. (e-f-g) Relative climate change signal for each of the three communities, computed as the difference between the SSP585 average over the 2070-2100 period and the *historical* average between 1850 and 1900. The latter is also used to normalise the signal and represent it as percentage.

436

## 4 Discussion and summary

437

### 4.1 Discussion

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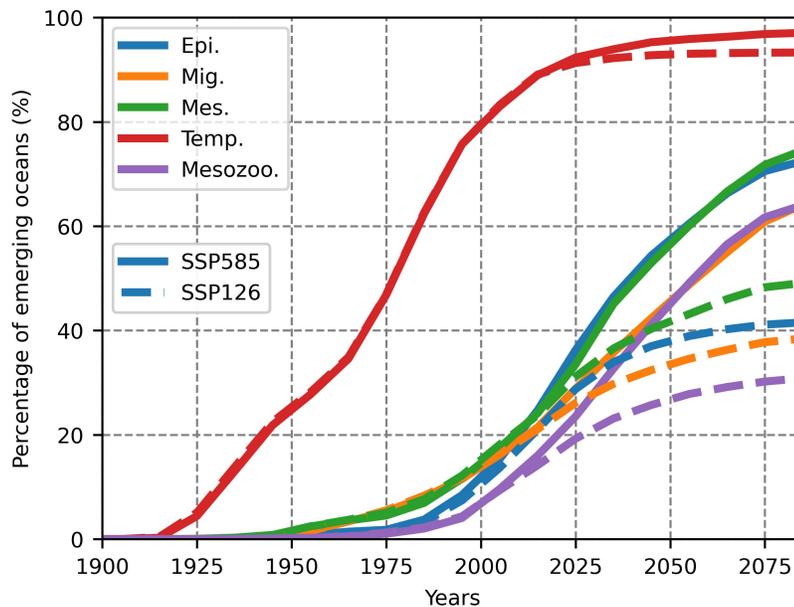
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In the above, regional ToE patterns have been investigated for the SSP5-8.5 scenario, in which 60% of the ocean surface will emerge by the end of the century. We have also shown that global mean time series emerge during the historical period (before 2020). One question that arises is whether mitigation policies can reduce the regional emergence.

442 Fig. 9 compares the cumulative percentage of the emerging ocean surface for temper-  
 443 ature, mesozooplankton and fish biomass climate change signal for both SSP5-8.5 and  
 444 SSP1-2.6 scenarios. While the scenario has a marginal impact on the ToE of SST, with  
 445 93% of the ocean surface emerging by the end of the century in SSP1-2.6 (compared to  
 446 97% in SSP5-8.5), it significantly reduces the surface impacted by climate change com-  
 447 pared to SSP5-8.5 for biological signals. By the end of the century, mesozooplankton emerges  
 448 in 31% of the ocean in the SSP1-2.6 scenario compared to 64% in the SSP5-8.5 scenario.  
 449 Similarly, epipelagic, migratory and mesopelagic fish biomass emerge in 41%, 38% and  
 450 49% of the ocean in the SSP126 scenario and in 72%, 64% and 75% in the SSP585 sce-  
 451 nario. Therefore, while the emergence of global fish biomass occurs during the histor-  
 452 ical period (prior to 2020), mitigation policies can maintain future marine ecosystems  
 453 within the range of their natural variations in most of the ocean's regions. These differ-  
 454 ences in the response of global mean and regional ToEs to mitigation are also a conse-  
 455 quence of the weaker noise in the former. Considering global time series, the weaker sig-  
 456 nal of the SSP1-2.6 scenario is sufficient to exceed the range of natural variability, which  
 457 is not the case when grid-scale ToEs are considered.



**Figure 9.** Cumulative percentage of the ocean surface in which the signal emerges for environmental variables and fish biomass in the SSP585 and the SSP126 scenarios

458 Our analysis also underscores the influence of the size class on the ToE. Notably,  
459 small ( $< 1$  cm) and large ( $> 50$  cm) epipelagic and mesopelagic organisms exhibits ear-  
460 lier emergence than their intermediate-sizes counterparts (about 20 cm). The later emer-  
461 gence of intermediate size organisms results from a larger noise within the epipelagic com-  
462 munity and a weaker signal within the mesopelagic community. On the other hand, mi-  
463 gratory fish of intermediate size fail to emerge due to a shift of their climate change sig-  
464 nal from positive (for small sizes) to negative (for large sizes). While understanding the  
465 changes in natural variability and in the response to climate change with size is beyond  
466 the scope of this study, it presents a compelling avenue for future investigation. Poten-  
467 tial approaches may involve decomposing biomass changes into their main contributions  
468 (predation, growth, advection, diffusion, Barrier et al. (2023)), or conducting sensitiv-  
469 ity analyses akin to those performed in Heneghan et al. (2019).

470 Furthermore, previous literature highlighted the large persisting uncertainties re-  
471 garding the climate change signal and ToE of biogeochemical variables. For example, us-  
472 ing large ensembles from four Earth System Models (ESMs), Schlunegger et al. (2020)  
473 findings point to robust climate change signal and ToE for SST across four different ESMs  
474 ensemble but far less consistency for chlorophyll concentration and carbon export. Un-  
475 certainties in the climate change signal of biogeochemical processes are well known (e.g.  
476 Bopp et al. (2022)) and can lead to large uncertainties on the fish biomass response to  
477 climate change, especially when the biogeochemical models are driven by the primary  
478 production, which is more uncertain than the planktonic biomass (Tittensor et al., 2021).  
479 Although APECOSM uses plankton biomass, which is more sounded as a forcing vari-  
480 able, it is reasonable to anticipate large uncertainties on the ToE estimates for fish biomass.  
481 Another source of uncertainties stems from the limited number of members used in our  
482 study. Due to the limited availability of the biogeochemical forcing variables required  
483 to run APECOSM, stored from the IPSL-CM6-LR model, only 6 members could be con-  
484 sidered, in comparison to the 30 members that were used in Schlunegger et al. (2020).  
485 Additionally, only one marine ecosystem model has been considered in this study. How-  
486 ever, large uncertainties remain in the mechanisms driving the response of marine ecosys-  
487 tems to climate change Heneghan et al. (2019). One way to address these uncertainties  
488 would be to derive multi-model ensembles of ToE estimates from the ensemble simula-  
489 tions that have been carried out as part of the Fisheries and Marine Ecosystem Model  
490 Intercomparison Project (FishMIP, Tittensor et al. (2018); Lotze et al. (2019); Titten-

491 sor et al. (2021)), which includes 16 climate-to-fish simulations, with 9 ecosystem mod-  
492 els forced by two different climate models.

493 Finally, we only considered the impact of climate change on the ecosystem. How-  
494 ever, fishing also has a significant impact on fish biomass. For example, using data from  
495 the Pacific tuna fisheries, Sibert et al. (2006) have shown that the fish biomass of tunas  
496 larger than 175 cm declined by about 40% at the end of the 1970s due to longline fish-  
497 eries. At the same time, purse-seine fishery began to affect smaller fish ( $\approx 75$  cm) in the  
498 1980s. This decline in fish biomass due to fishing would superimpose on the decline due  
499 to climate change, inevitably affecting the estimated ToE of marine fish biomass. Recog-  
500 nising this, the FishMIP community has begun to develop a new socio-economic scenario  
501 framework derived from the SSPs, called Ocean System Pathways (the OSPs, Maury et  
502 al. (2024), this issue). The OSPs are designed to project the spatio-temporal dynamics  
503 of fisheries and marine ecosystems. Using this innovative scenario framework, it will be  
504 possible to explore the impact of both fisheries and climate change on the emergence of  
505 fish biomass changes, and to identify potential synergies between these factors. OSPs  
506 could be used to address the additive effects of fishing on the emergence of marine ecosys-  
507 tems.

## 508 4.2 Summary

509 This study represents the first attempt to estimate the Time of Emergence (ToE)  
510 of climate change driven in fish biomass changes. ToE refers to the moment when these  
511 changes have or will emerge from the natural background variability. Using ensemble cli-  
512 mate to fish simulations based on the APECOSM ecosystem model forced with the IPSL-  
513 CM6-LR Earth System physical and biogeochemical outputs, we determine the ToE of  
514 the epipelagic, migratory and mesopelagic communities and their two main environmen-  
515 tal drivers, temperature and mesozooplankton.

516 Globally averaged fish biomass signals emerge during the historical period across  
517 all three communities. The epipelagic and mesopelagic fish biomass decline mirrors that  
518 of mesozooplankton, suggesting a bottom-up control of their response to climate change.  
519 However, the signal of epipelagic fish biomass emerges earlier (1950) than that of meso-  
520 zooplankton (2000) due to a stronger signal in the early 20th century, likely related to  
521 trophic amplification induced by an early emerging surface warming (1915). Conversely,

522 the trophic amplification for the mesopelagic community lags due to a delayed warm-  
523 ing in the mesopelagic zone (500-1000 m), resulting in a later emergence (2000). While  
524 global migratory fish biomass also emerges during the historical period, its signal is con-  
525 siderably weaker than that of the other two communities.

526 Regional emergence lags behind that of global mean signals. For example, the peak  
527 of regional mesozooplankton emergence occurs 30 years later than that of the global mean  
528 mesozooplankton, 75 years for epipelagic and 35 years for migratory and mesopelagic fish  
529 communities. This delay can be tracked back to a considerably weaker globally-averaged  
530 noise compared to regional one. Consequently, mitigation policies could strongly reduce  
531 the ocean surface where biogeochemical and biological signals emerge (about 60% in the  
532 SSP5-8.5 scenario and about 30% in the SSP1-2.6 scenario).

## 533 **Open Research Section**

534 The APECOSM model is available here: [https://github.com/apecosm/apecosm](https://github.com/apecosm/apecosm-private)  
535 `-private`. Access will be provided on request to the corresponding author. The version  
536 used in this study is `c0a910b8`.

537 The APECOSM configuration files are available on Zenodo: [https://doi.org/](https://doi.org/10.5281/zenodo.10454379)  
538 `10.5281/zenodo.10454379`

539 All the Python scripts used to analyse the results are available here: [https://github](https://github.com/barriern/stage-maelys)  
540 `.com/barriern/stage-maelys`.

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Figure 9.

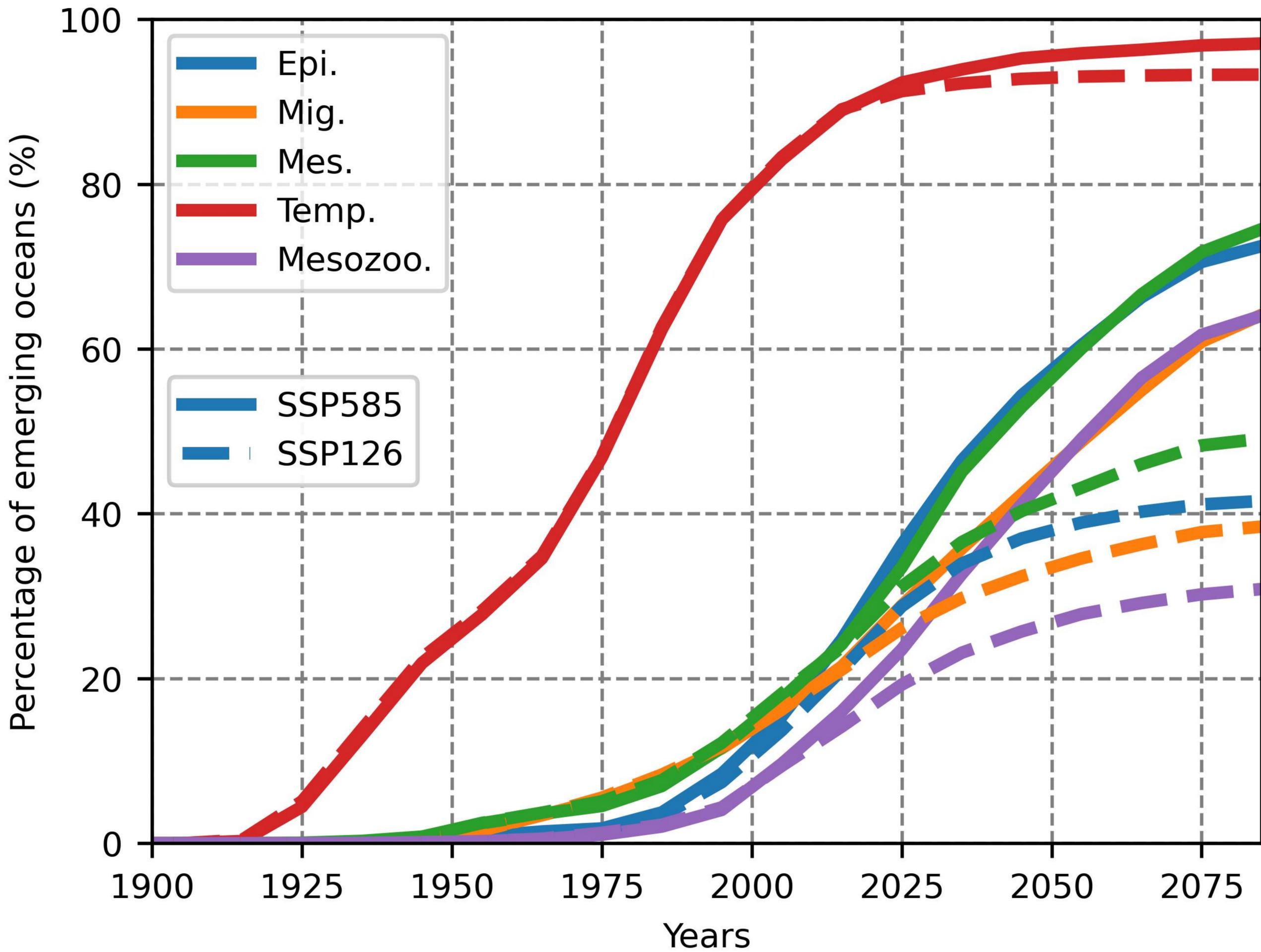
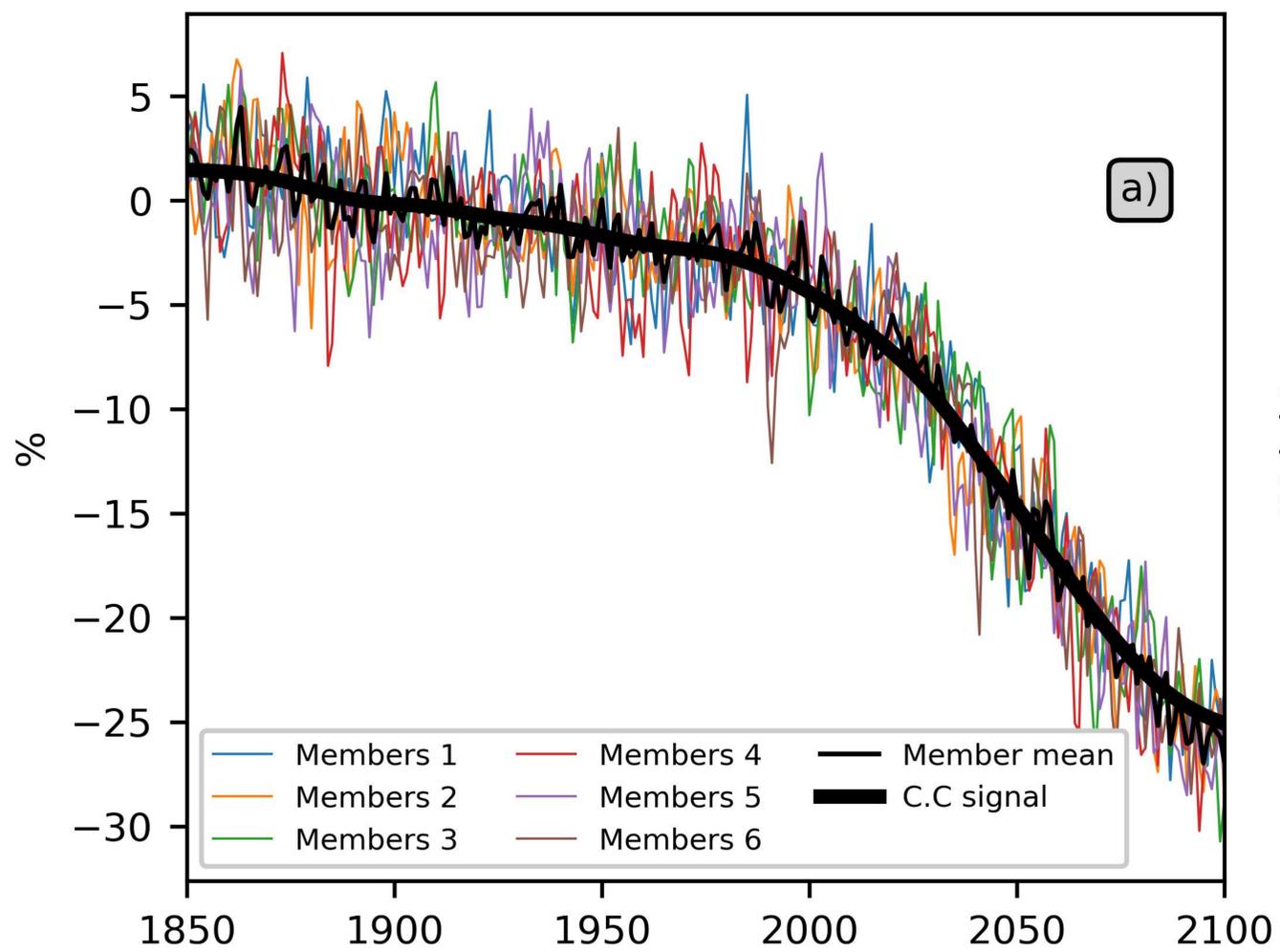
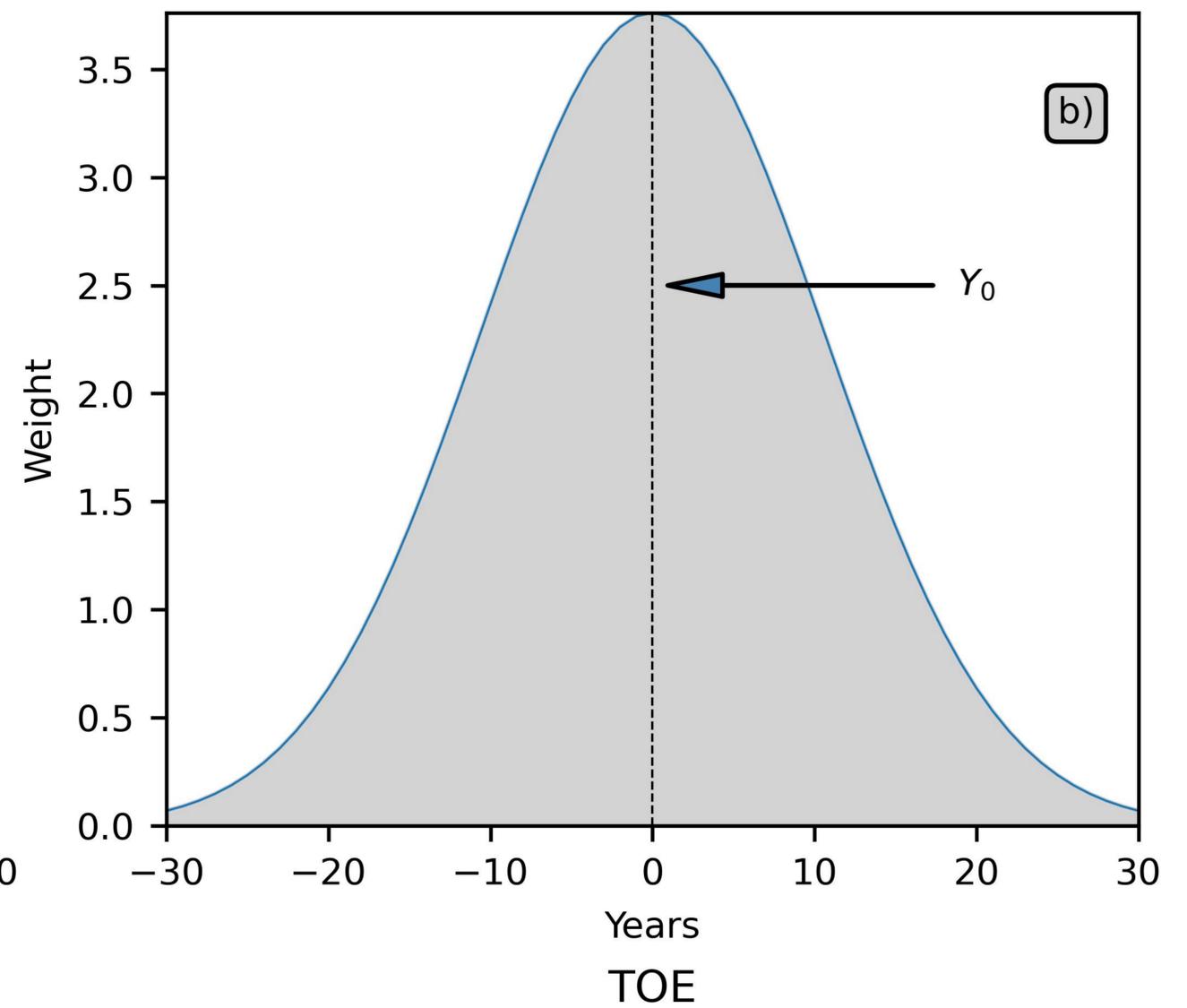


Figure 1.

Raw time-series



Gaussian kernel



Anomaly time-series

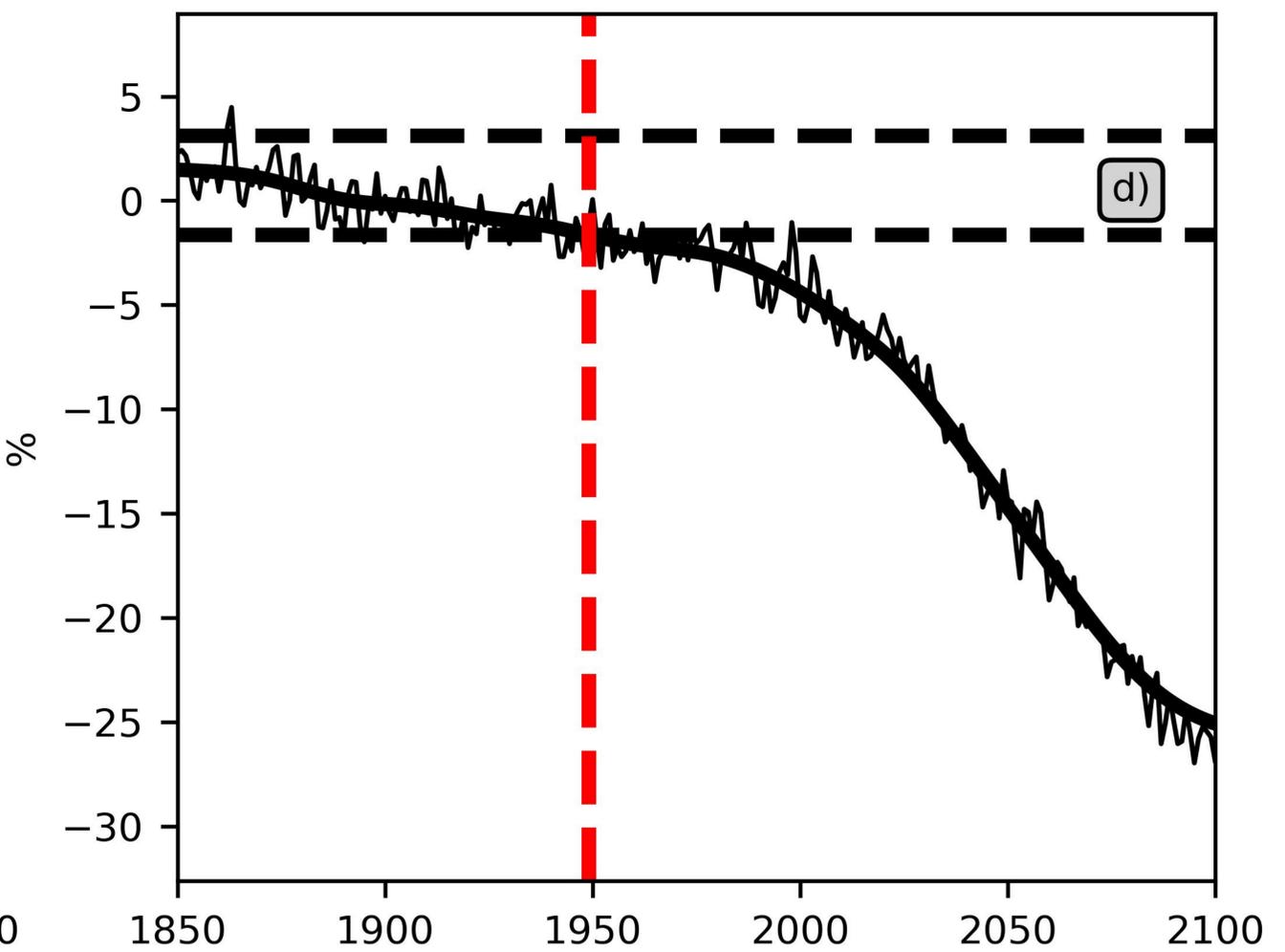
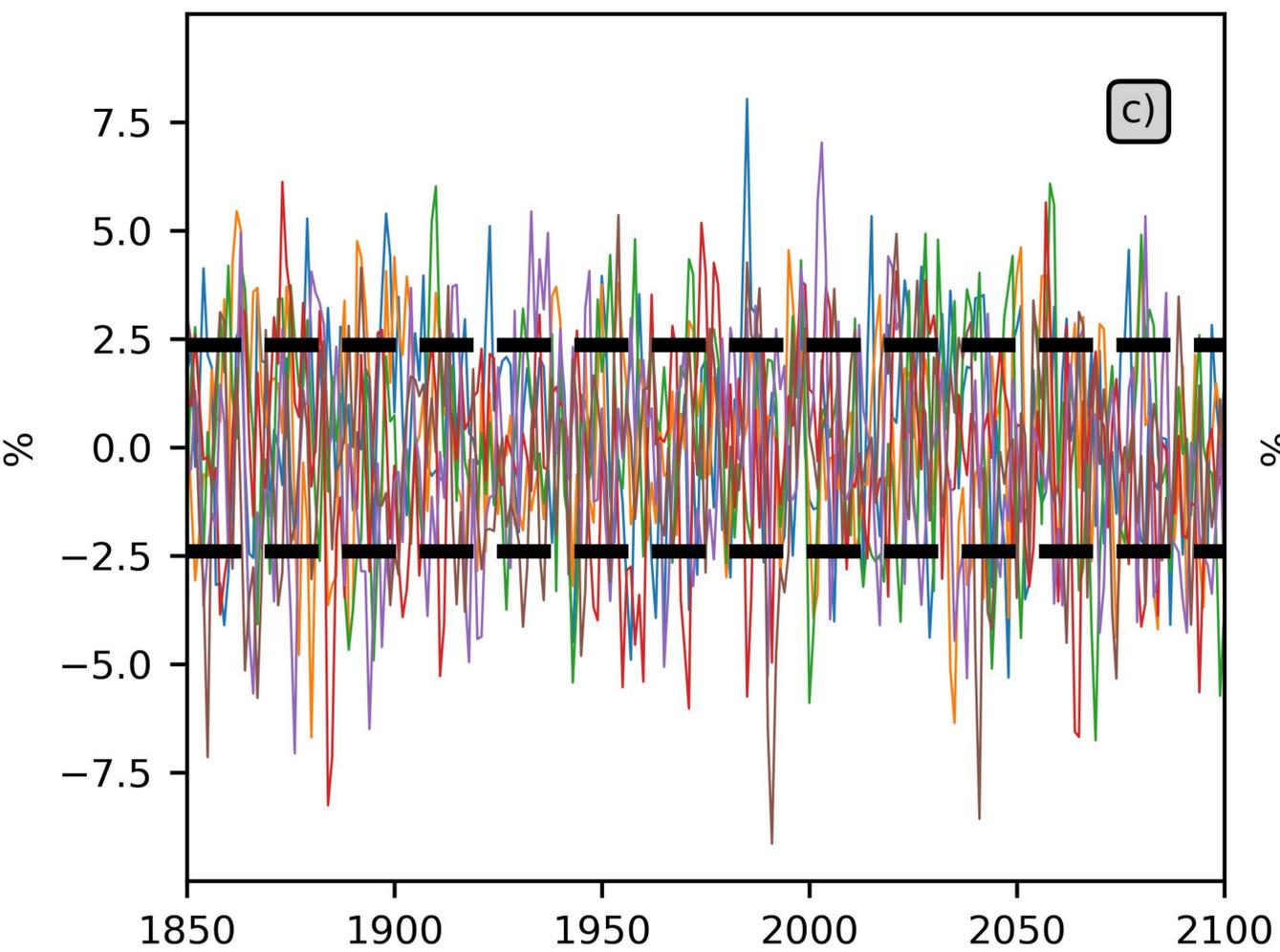


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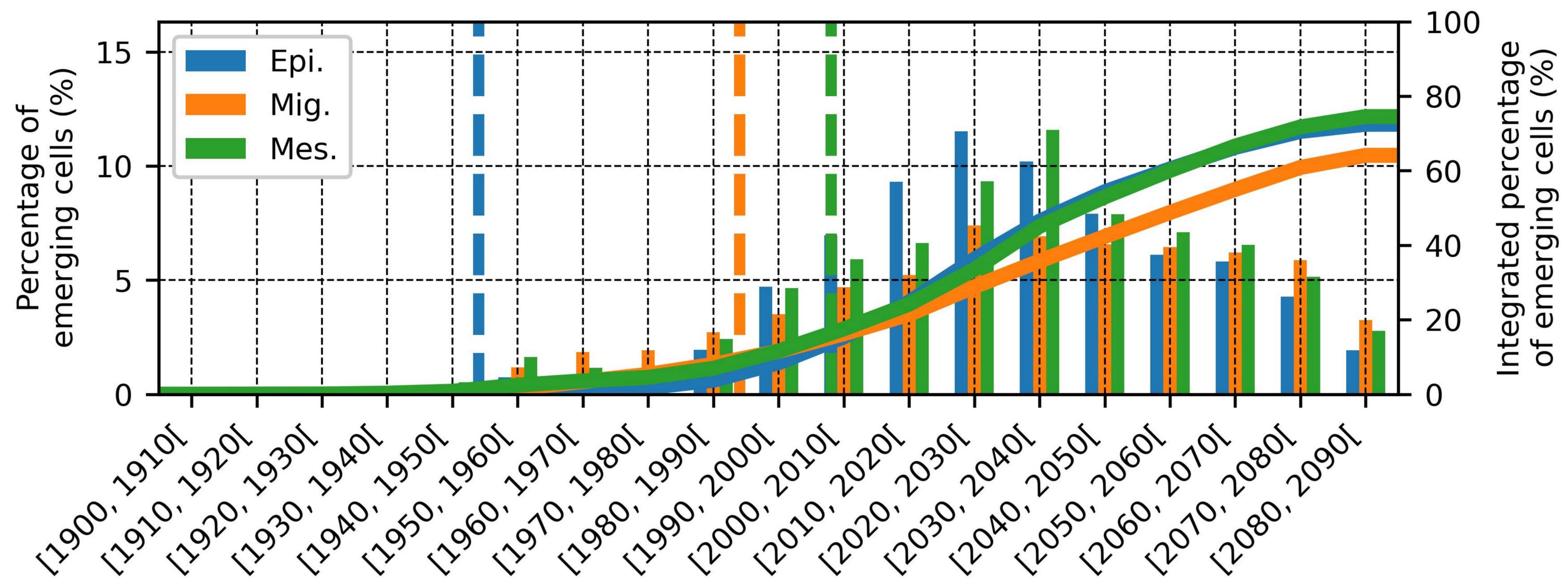
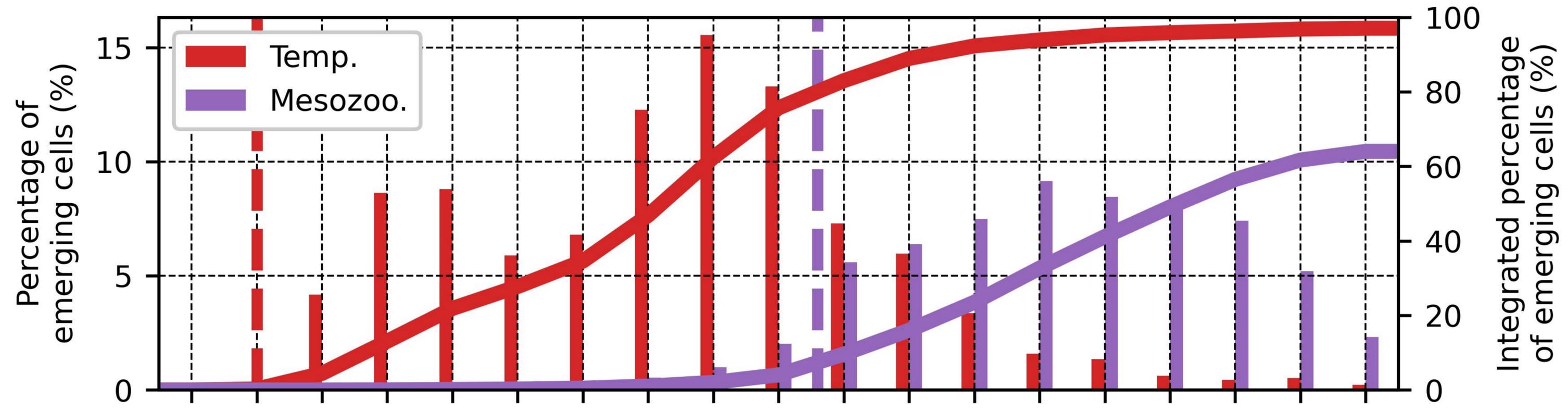


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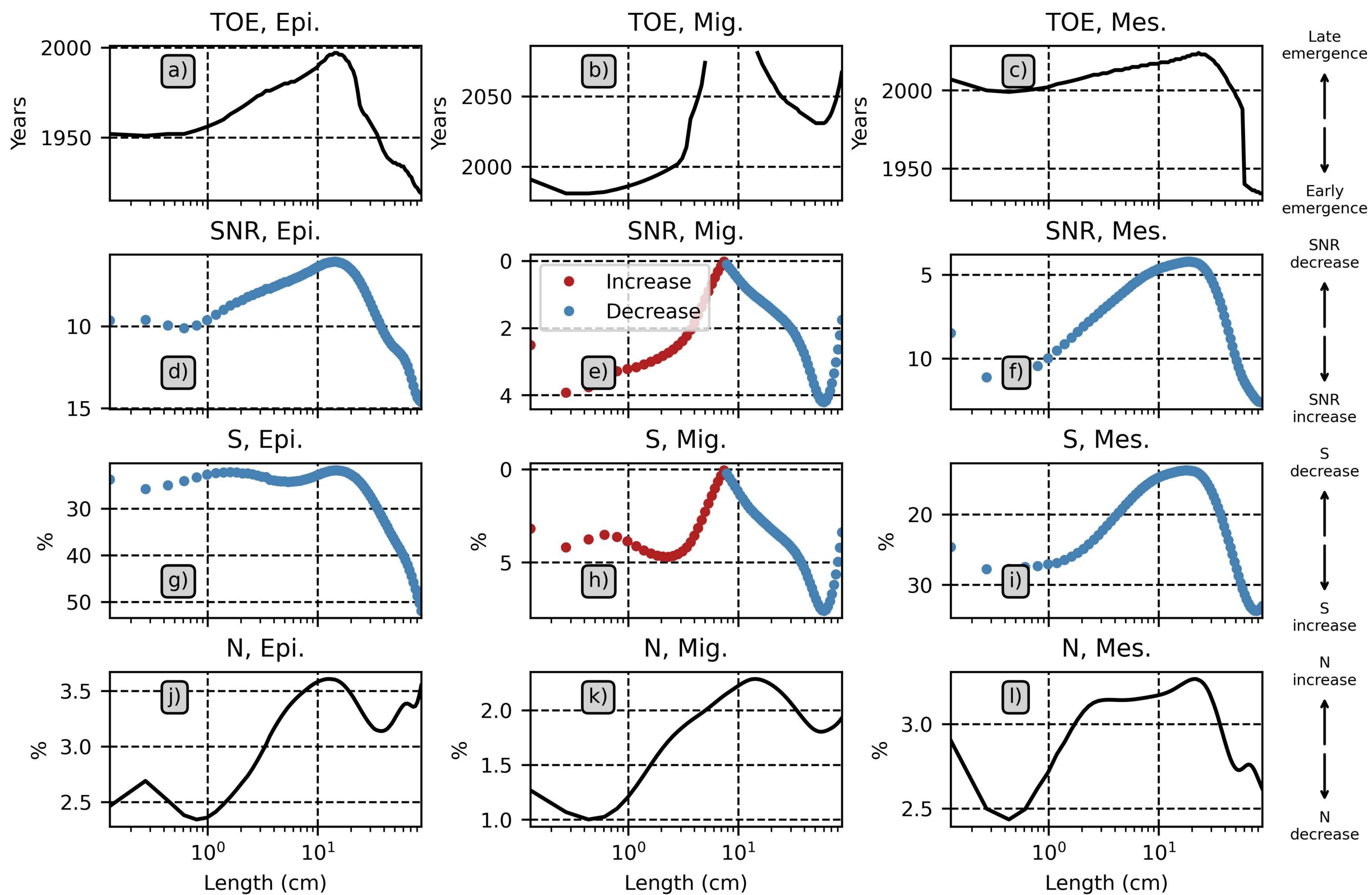
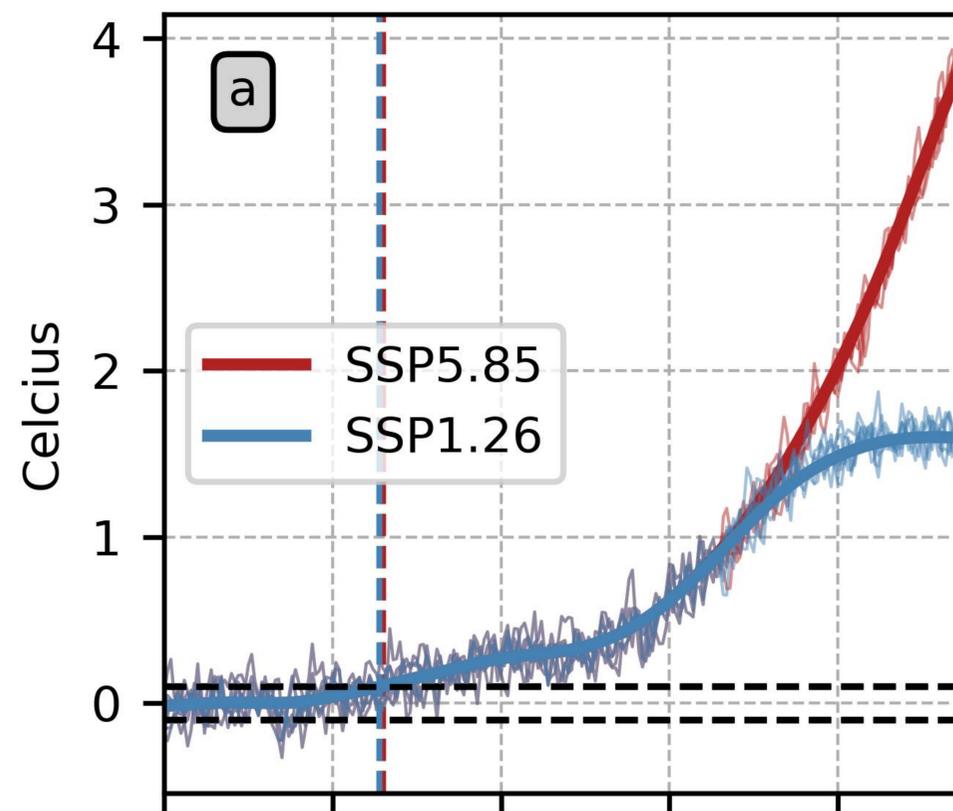
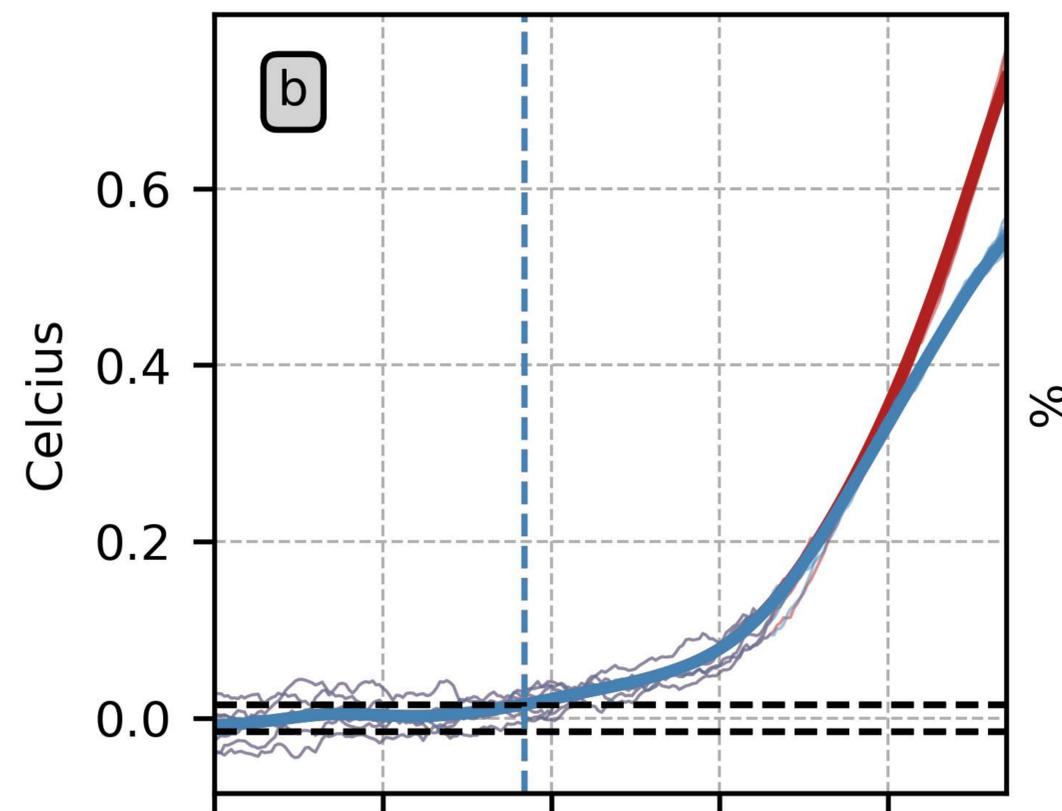


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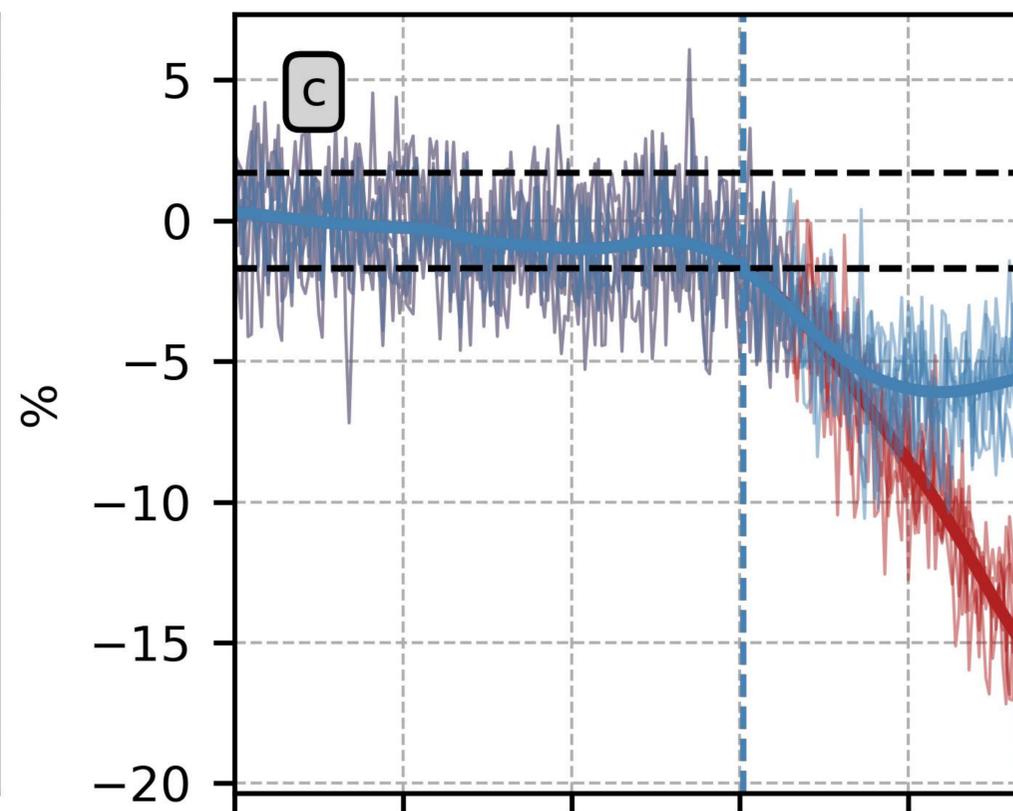
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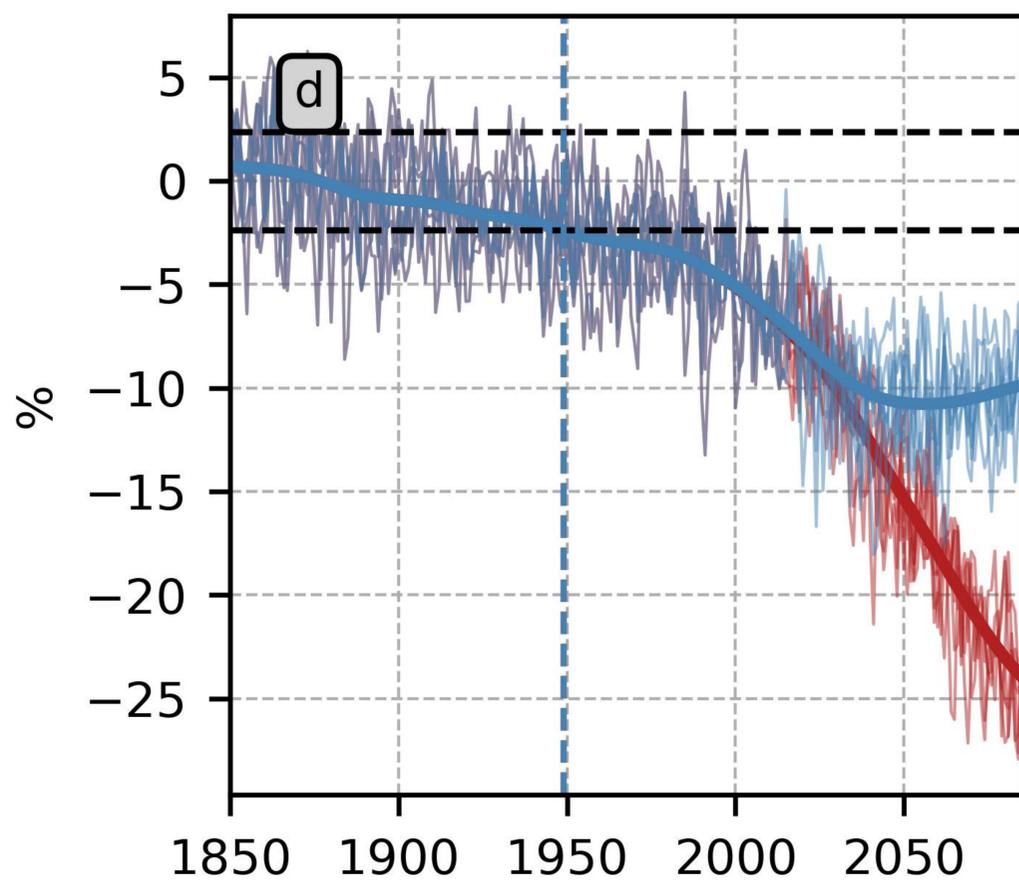
Temp (500-1000m)



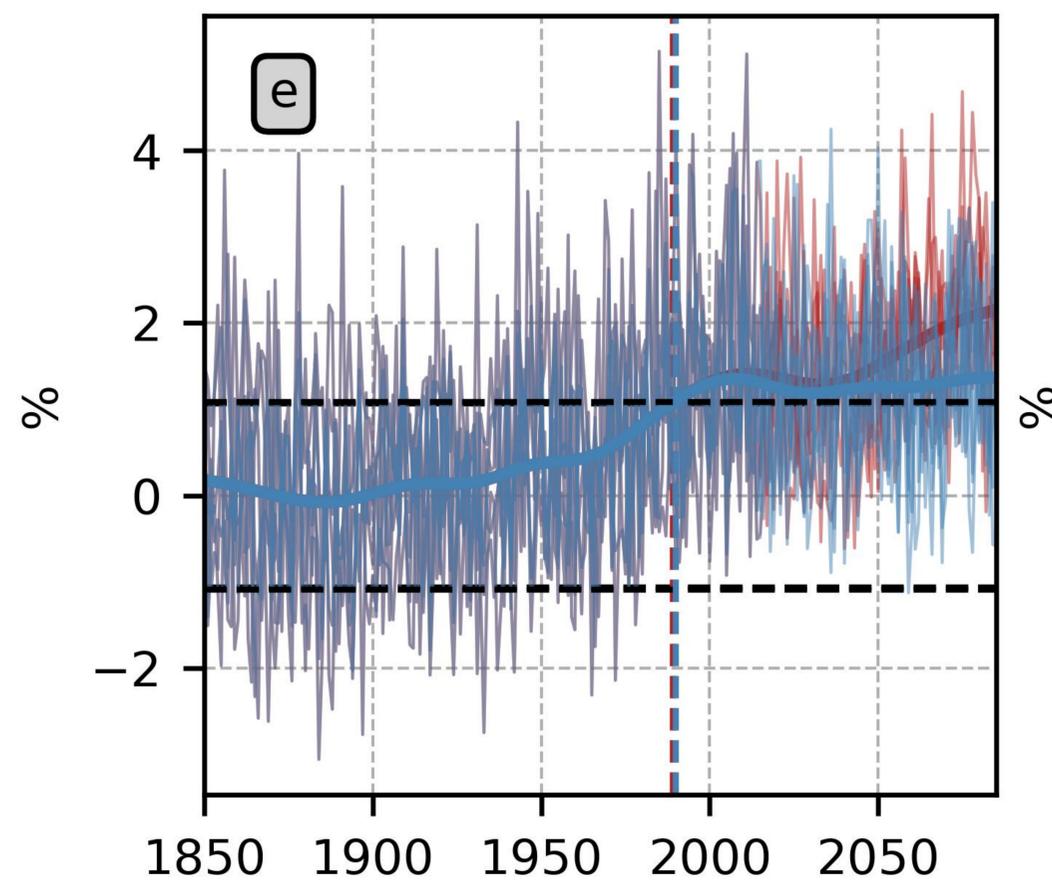
Meso-zoo



Epi.



Mig.



Mes.

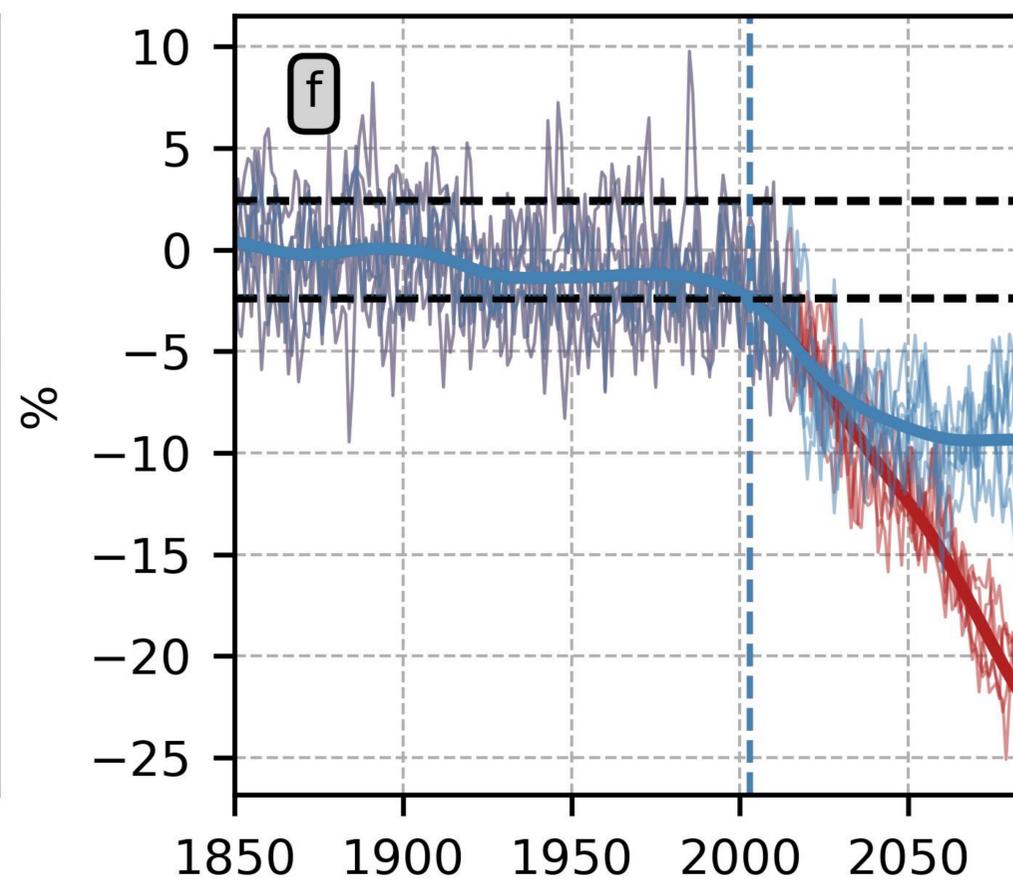
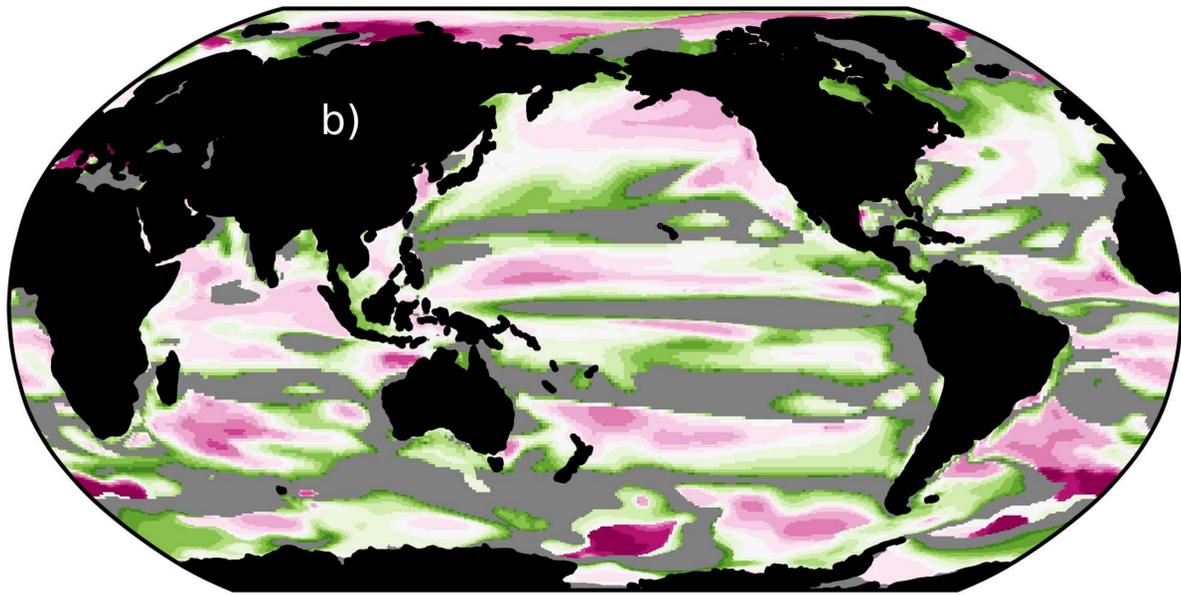
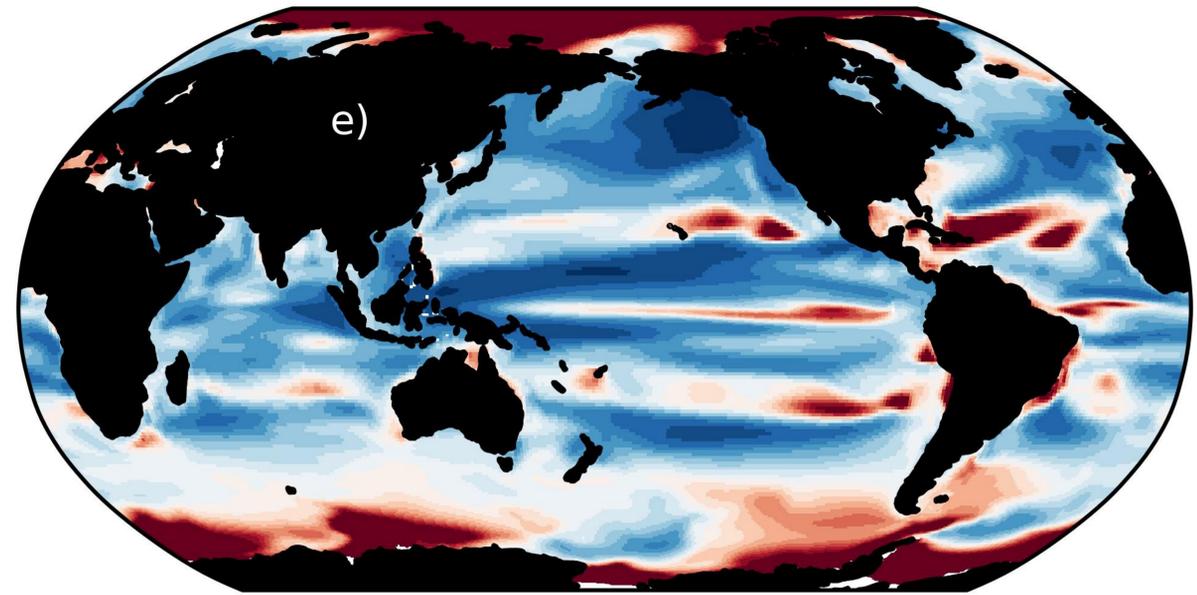


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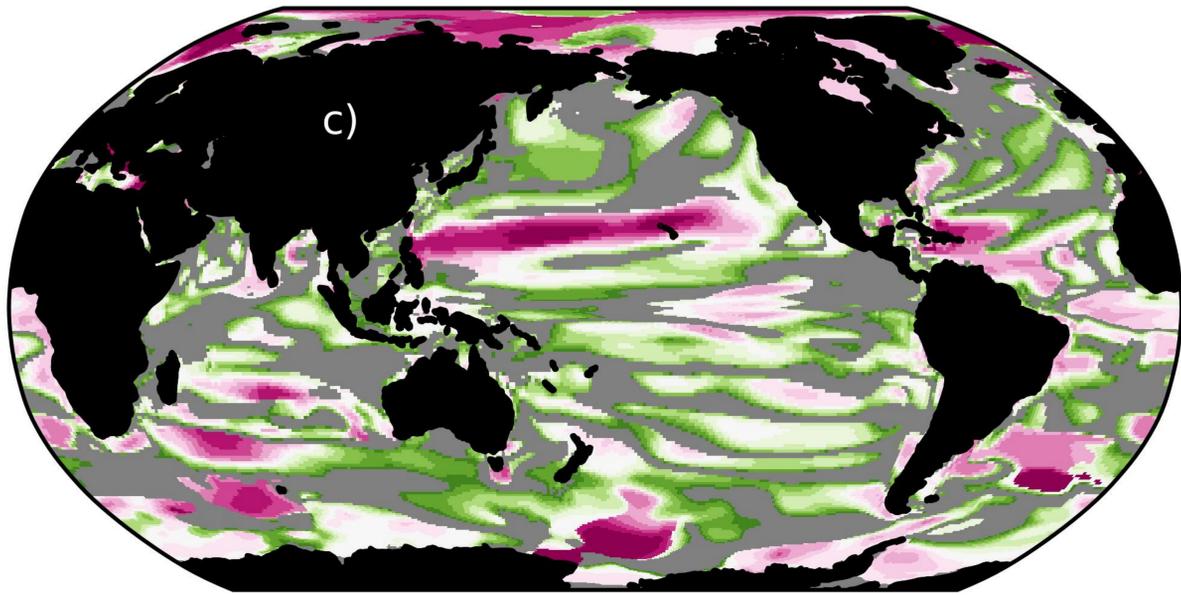
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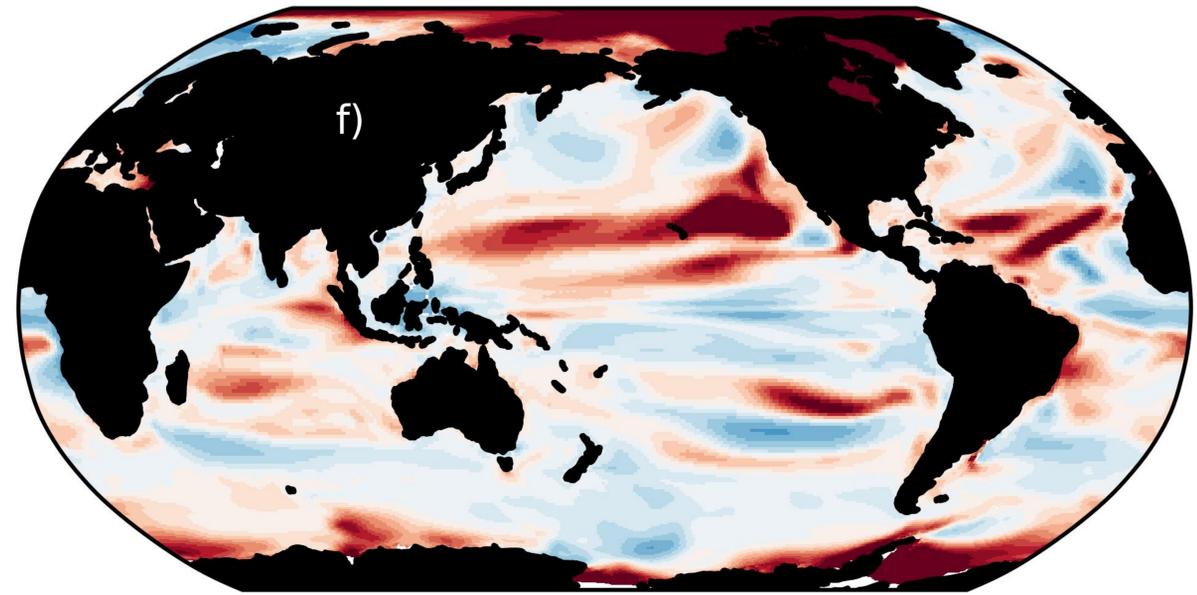
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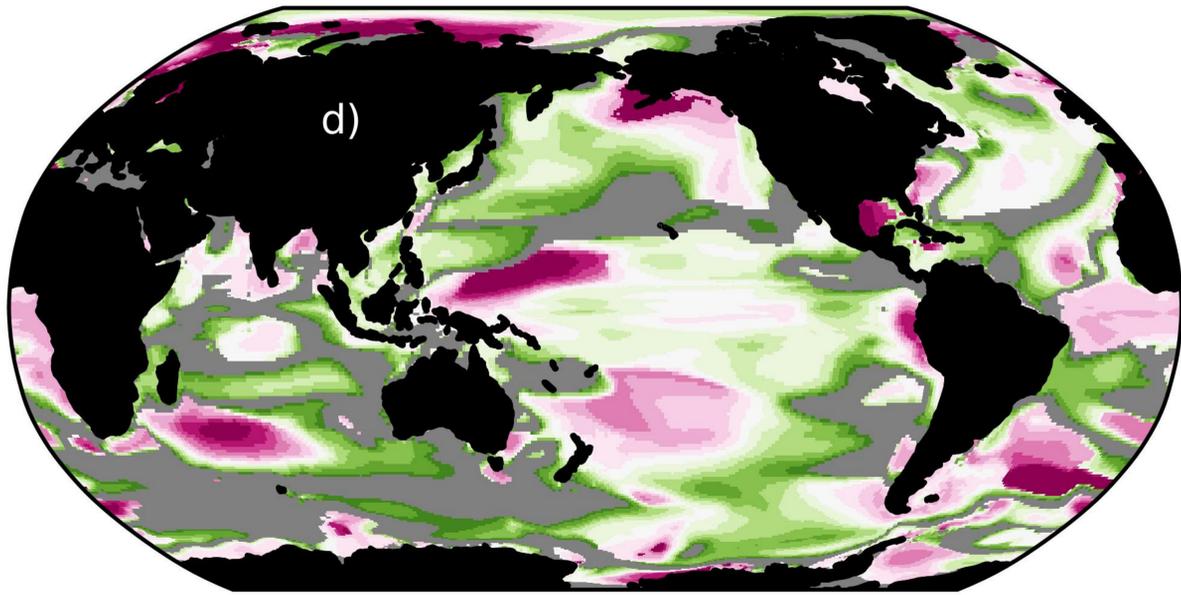
Migrants



Migrants



Mesopelagic



Mesopelagic

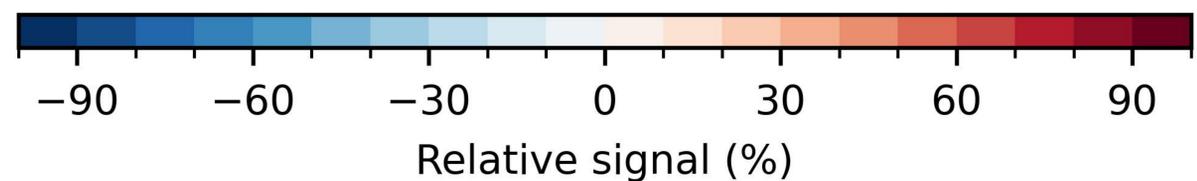
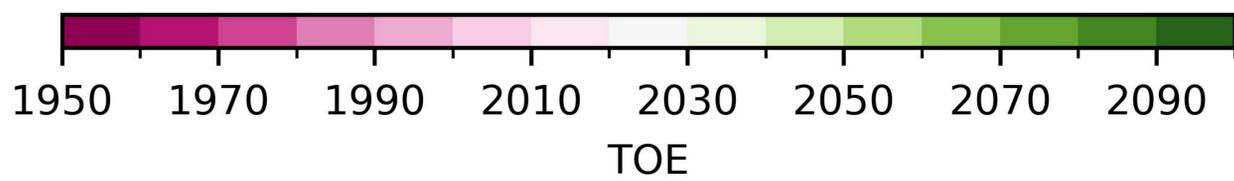
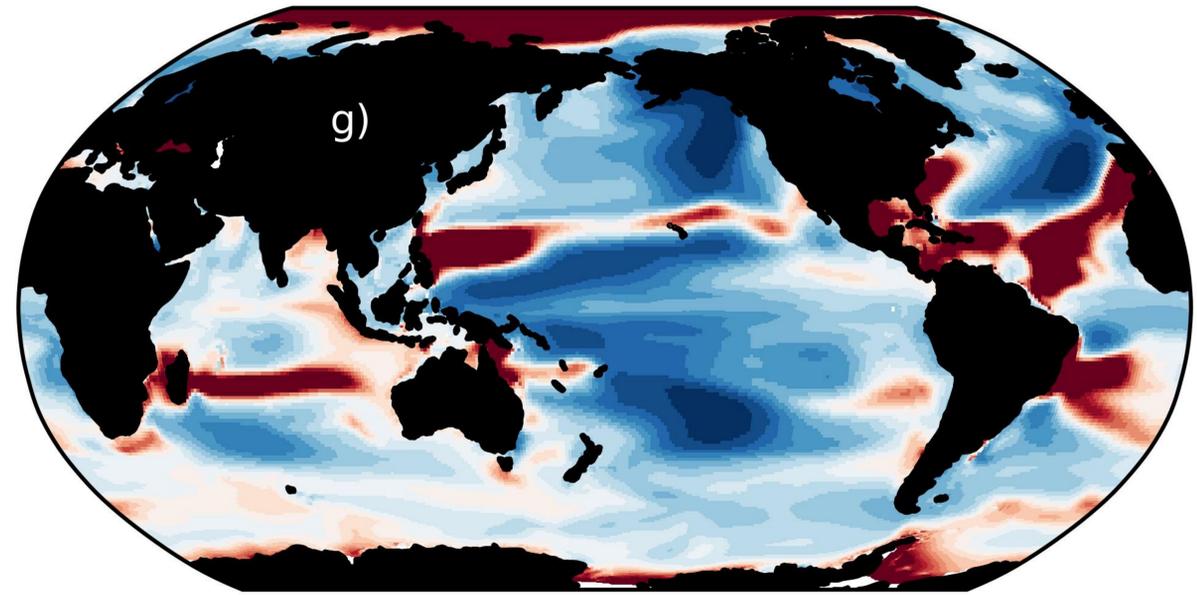
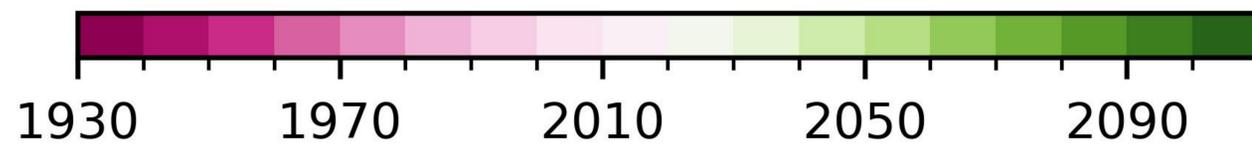
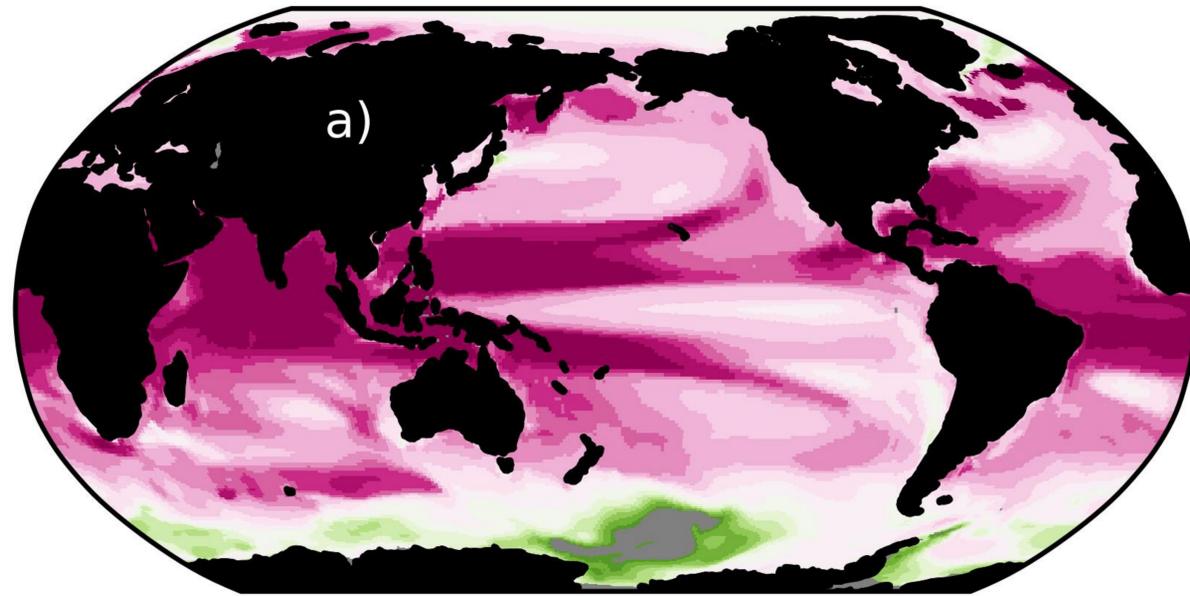
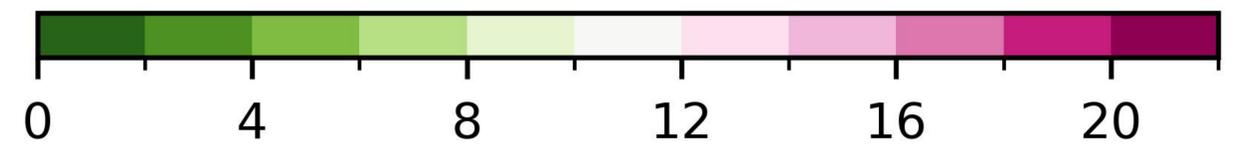
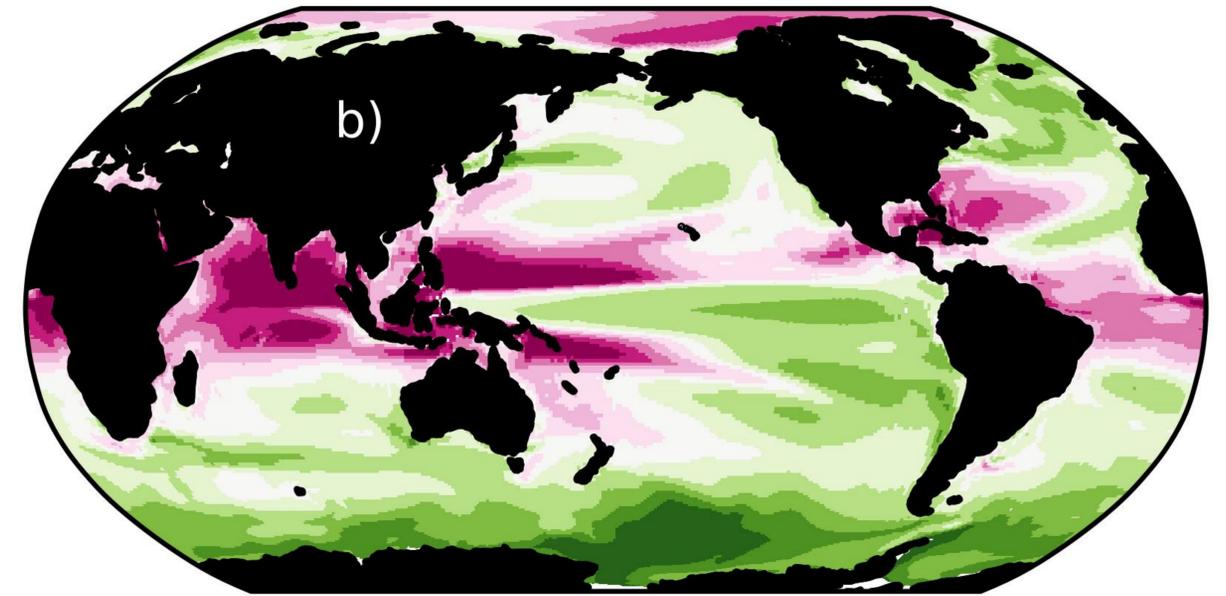


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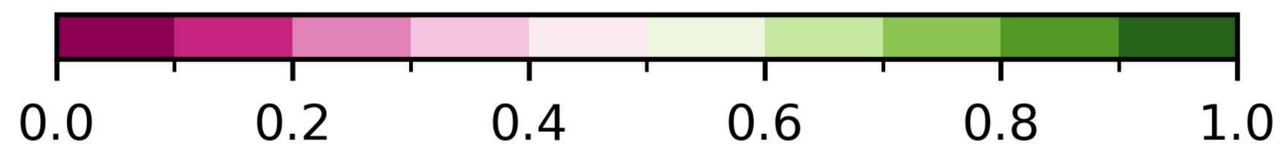
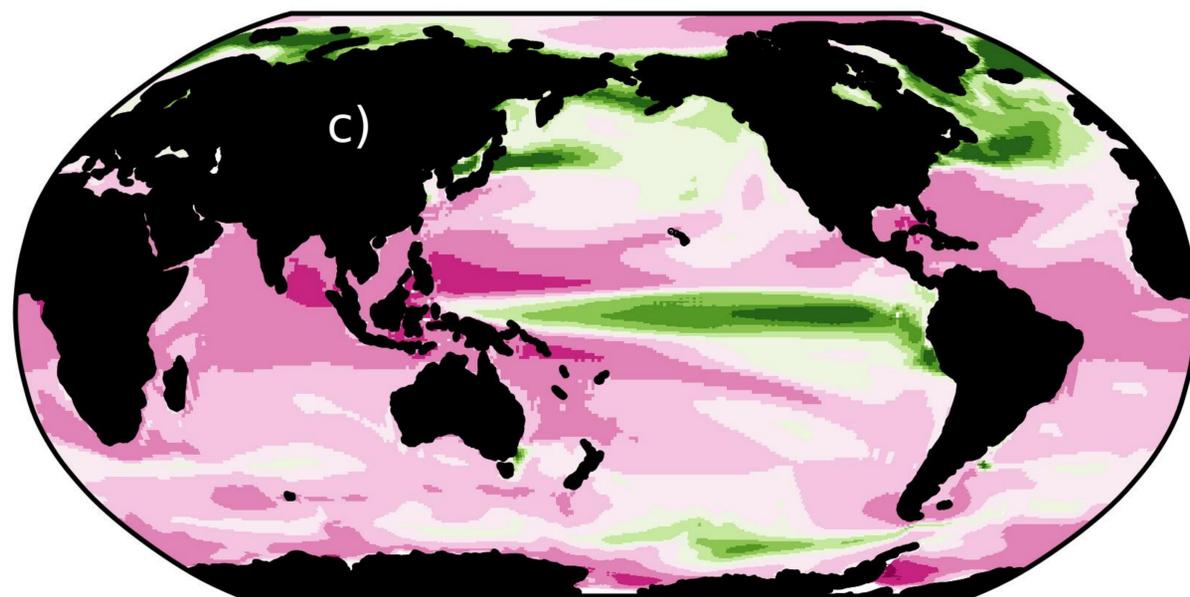
Time of emergence



|Signal| to Noise ratio

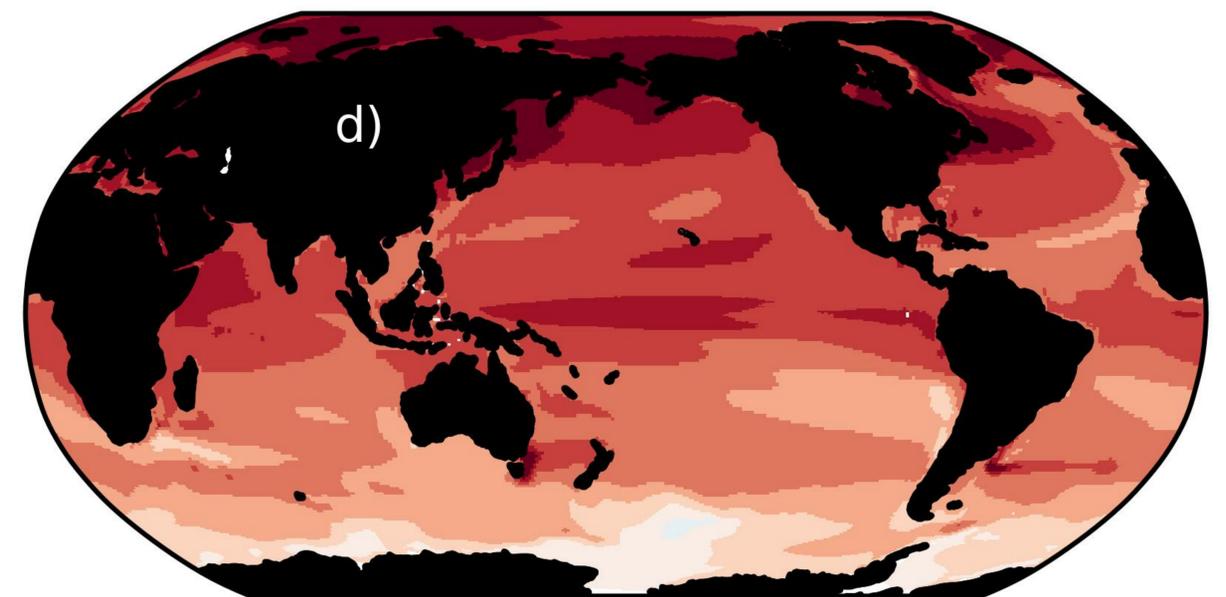


Noise



C

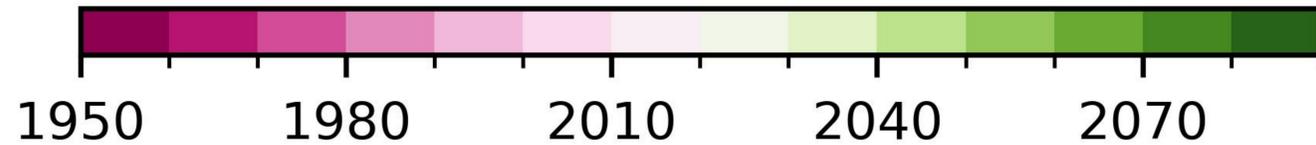
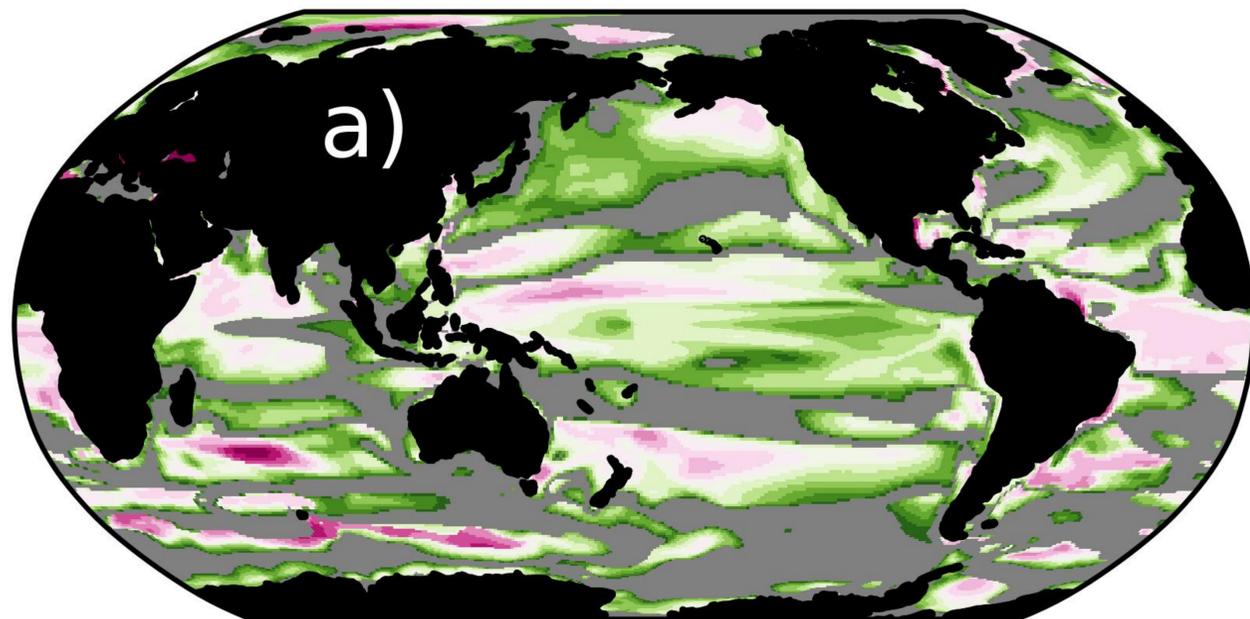
Signal



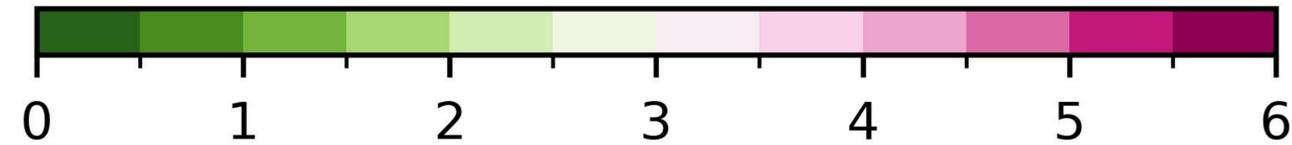
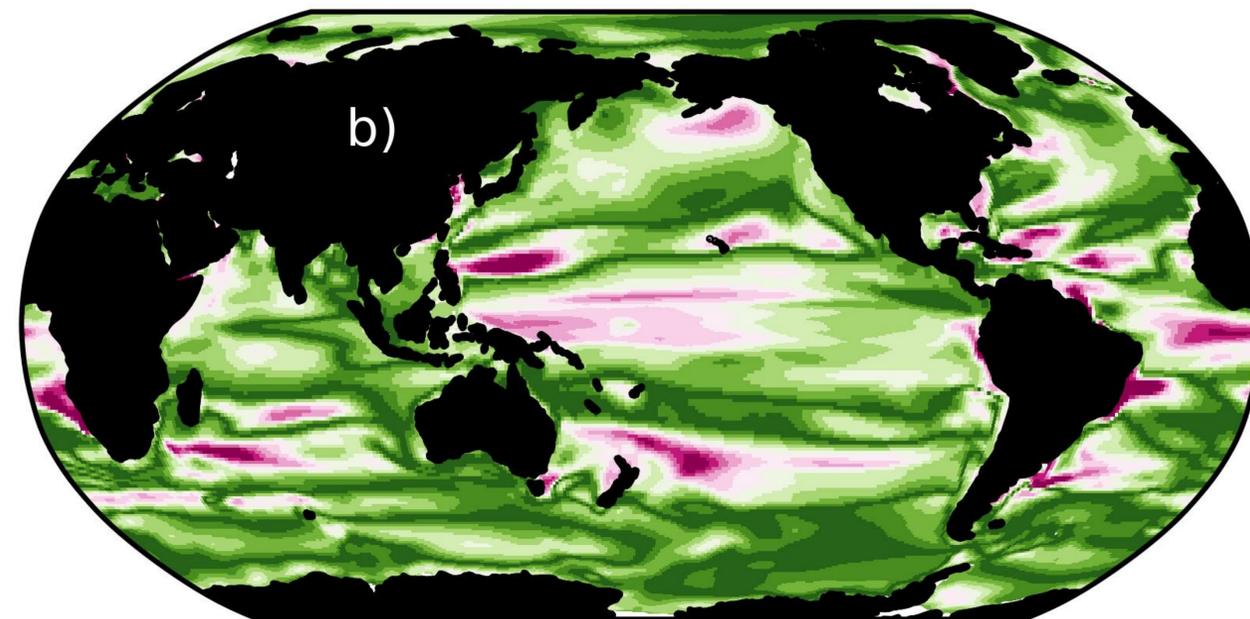
C

Figure 7.

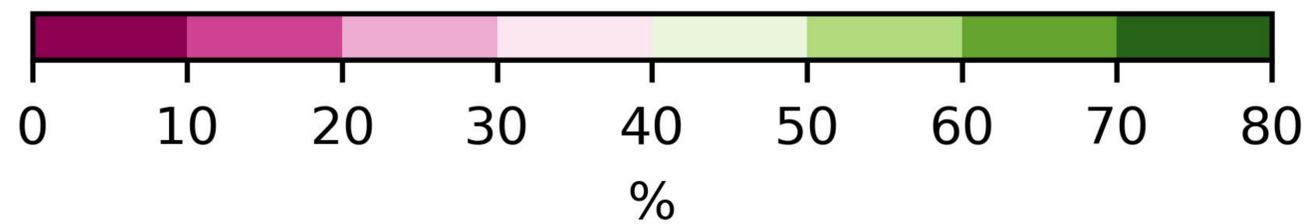
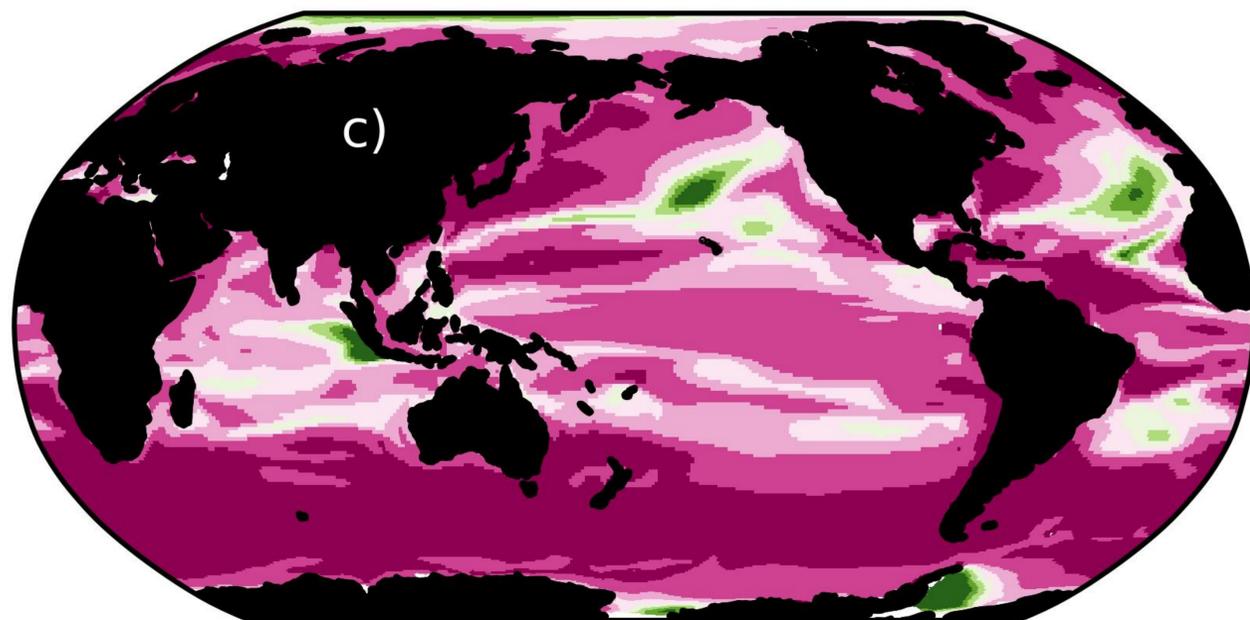
Time of emergence



|Signal| to Noise ratio



Relative Noise



Relative Signal

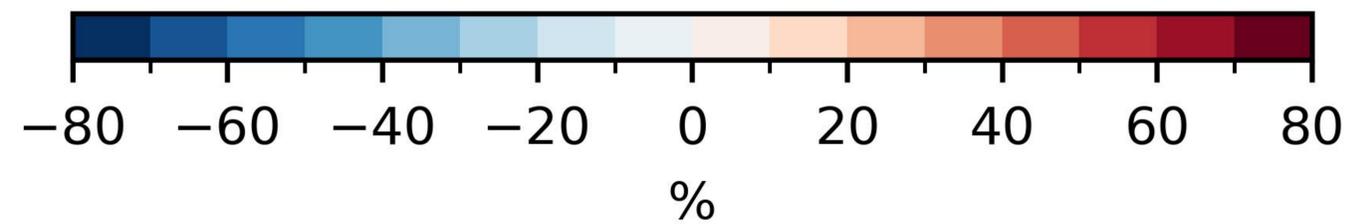
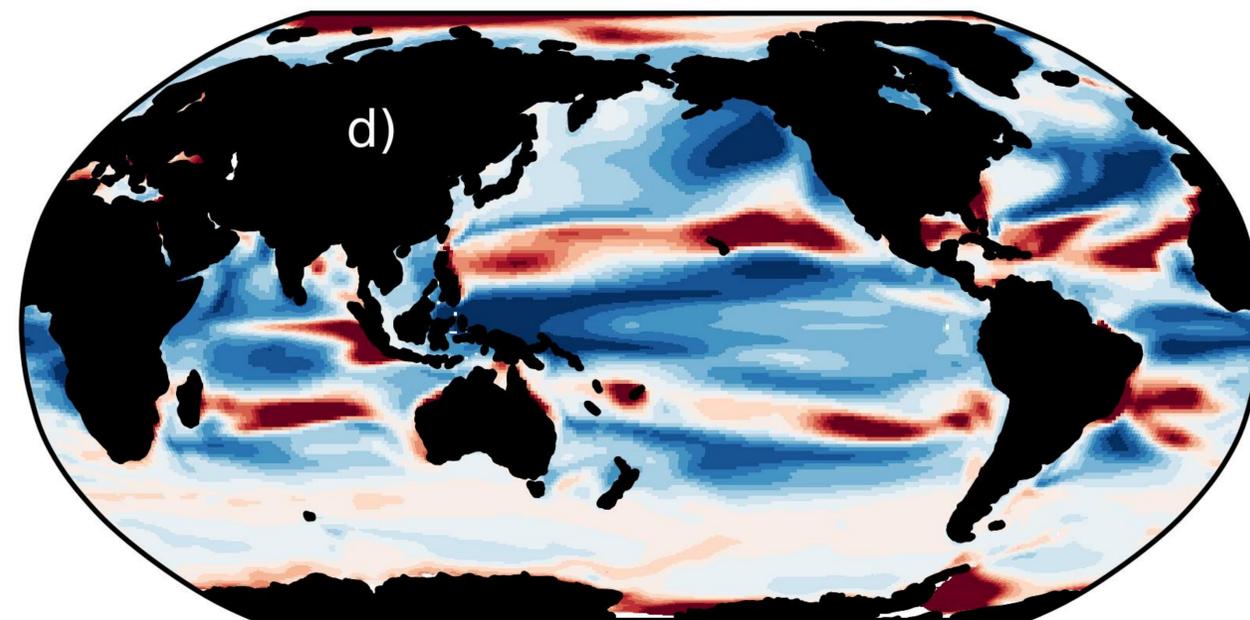


Figure 5.

