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# Global decline of pelagic fauna in a warmer ocean

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Alejandro Ariza<sup>1\*</sup>, Matthieu Lengaigne<sup>1</sup>, Christophe Menkes<sup>2</sup>, Anne Lebourges-Dhaussy<sup>3</sup>, Aurore Receveur<sup>4</sup>, Thomas Gorgues<sup>5</sup>, Jérémie Habasque<sup>3</sup>, Mariano Gutiérrez<sup>6</sup>, Olivier Maury<sup>1</sup>, and Arnaud Bertrand<sup>1</sup>.

<sup>1</sup>MARBEC, Univ. Montpellier, CNRS, Ifremer, IRD, Sète, France.

<sup>2</sup>ENTROPIE, IRD, CNRS, Ifremer, Université de la Réunion, Université de la Nouvelle-Calédonie, Nouméa, New Caledonia

<sup>3</sup>LEMAR, UBO, CNRS, IRD, Ifremer, Plouzané, France.

<sup>4</sup>CESAB-FRB, Montpellier, France

<sup>5</sup>LOPS, UBO, CNRS, IRD, Ifremer, Plouzané, France

<sup>6</sup>Instituto Humboldt de Investigación Marina y Acuícola, Lima, Peru.

\*Corresponding author: [alejandro.ariza@ird.fr](mailto:alejandro.ariza@ird.fr)

**Abstract.** Pelagic fauna is expected to be impacted under climate change according to ecosystem simulations. However, the direction and magnitude of the impact is still uncertain and still not corroborated by observational-based statistical studies. Here we compile a global underwater sonar database and 20 ocean climate projections to predict the future distribution of sound-scattering fauna around the world's oceans. We show that global pelagic fauna will be seriously compromised by the end of the 21<sup>st</sup> century, if we continue under the current greenhouse emission scenario. Low and mid latitudes are expected to lose from 3 to 22% of animal biomass due to the expansion of low-productive systems, while higher latitudes would be populated by present-day temperate fauna, supporting conclusions drawn from ecosystem simulations. We further show that strong-mitigation measures to contain global warming below 2°C would reduce these impacts to less than half.

26 The pelagic zone—the vast volume of open-ocean water from the surface to the seabed—is the largest  
27 living space of the planet. This three-dimensional environment holds half of the global primary production  
28 and sustains most of the animal biomass on earth<sup>1,2</sup>. Dominated by small crustaceans, fish, molluscs and a  
29 variety of gelatinous life-forms, this mid-trophic level community channels primary production to the top  
30 of the food web<sup>3</sup>, being the fundamental forage base for apex predators such as marine mammals, seabirds,  
31 and major commercial fish stocks<sup>4,5</sup>. In addition, a substantial proportion of mid-trophic level fauna is  
32 involved in diel vertical migration<sup>6</sup>, the largest movement of animals on earth<sup>7</sup>, and a fundamental pathway  
33 of biomass exchange between epipelagic (0-200 m) and mesopelagic (200-1000 m) waters<sup>8,9</sup>. By respiring,  
34 defecating, and occasionally being predated at depth, vertical migrants inject large amounts of carbon into  
35 the ocean interior, contributing to the sequestration of atmospheric CO<sub>2</sub><sup>10-12</sup>.

36 Projections of ocean warming, deoxygenation and primary production declines in response to climate  
37 change<sup>13,14</sup> have led to concerns about the future evolution of mid-trophic level fauna. This fostered the  
38 emergence of global marine ecosystem models that include this critical component in their simulations<sup>15</sup>.  
39 These models, forced by future physical and biogeochemical oceanic model outputs, are used to simulate  
40 marine ecosystems, from primary producers to top predators. Overall, ecosystem models project a global  
41 decline of animal biomass by the end of the 21<sup>st</sup> century, primarily driven by increasing temperature and  
42 decreasing primary production<sup>16-19</sup>. However, because of their complex design and diverse representation  
43 of ecological processes<sup>15</sup>, these models still project a wide range of directional changes at regional scale,  
44 even within the same climate simulation experiment<sup>20</sup>. Most importantly, ecosystem models lack ground  
45 truth validation of mid-trophic level fauna at global-scale.

46 Primary producers and other plankton components can be remotely sensed from space or continuously  
47 sampled from moorings and ships of opportunity<sup>21,22</sup>, however, research on mid-trophic level fauna requires  
48 large sampling nets and complex deep water operations<sup>23,24</sup>. As a result, knowledge on its distribution,  
49 diversity, and response to environmental factors has long been limited to regional research or to global  
50 reviews based on variable methodological approaches<sup>25,26</sup>. Observations with ship-borne acoustic  
51 echosounders are an alternative approach that, while not taxonomically precise, provide consistent and  
52 large-scale data on predominantly mid-trophic level fauna from pelagic ecosystems<sup>27,28</sup>. These observations  
53 are increasingly available over large ocean regions<sup>29,30</sup> and have recently permitted to revise estimates of  
54 global mesopelagic fish biomass<sup>31</sup> as well as to describe sound-scattering and migration in major ocean  
55 basins<sup>32,33</sup>. Linear statistical modelling between environmental drivers and the intensity of sound-scattering  
56 layers also allowed for an assessment of future mesopelagic fish biomass in response to climate change<sup>34</sup>.  
57 This study indicates that ocean warming and decreased primary production is expected to cause an increase  
58 of fish biomass by the end of the 21<sup>st</sup> century<sup>34</sup>, in contradiction with projections from all ecosystem models

59 forced under comparable climate scenarios<sup>16–19</sup>. Such discrepancies between statistical and mechanistic  
60 modelling illustrate that there is still no consensus on the fate of pelagic fauna under multiple global  
61 climate stressors.

62 To shed light on this issue, we constructed a global atlas of sound-scattering mid-trophic level fauna, based  
63 on the largest acoustic dataset available to date. This database includes fundamental oceanic biomes that  
64 were previously unrepresented, such as coastal upwelling, oxygen-minimum, and equatorial zones. The  
65 structure and distribution of mid-trophic level fauna is projected worldwide for the present period, and  
66 under different future climate change scenarios, based on the latest generations of Earth system models  
67 from the Coupled Model Intercomparison Project Phase 5 and 6 (CMIP5<sup>13</sup> and CMIP6<sup>14</sup>). These projections  
68 relied on twenty different climate simulations, an optimized suite of environmental predictors, and non-  
69 linear statistical modelling based on machine learning. With this design, we project strong declines of mid-  
70 trophic level fauna in a warmer and less productive ocean by the end of the 21<sup>st</sup> century, corroborating  
71 ecosystem model projections with an observationally-based approach.

72 **Acoustic seascape classification.** We compiled a database with publicly available acoustic data at 38 kHz,  
73 the most widely used frequency for observing mid-trophic level fauna at epipelagic and mesopelagic  
74 depths. The database covered more than 350,000 km around the globe, extended from 20 to 750 m depth,  
75 and spanned from year 2001 to 2020 ([Supplementary Table 1](#)). The ocean was gridded into 4x4 degree cells  
76 and average day and night profiles were computed for each cell ([Extended Data Fig. 1](#)). In total, we  
77 obtained 459 cells, which represented 16% of the ocean surface, from open to coastal-boundary systems  
78 and from 66°S to 50°N. We transformed the vertically discretized data of profiles into continuous curves  
79 and explored the variation of these curves—day and night together—using functional principal component  
80 analysis<sup>35</sup>. The principal components that accounted for more than 90% of the total backscatter variance of  
81 profiles were used to classify the data through hierarchical clustering (see [Methods](#) and [Extended Data](#)  
82 [Figs. 2 and 3](#)).

83 We identified six acoustic seascape classes associated with subpolar, gyre, subtropical, temperate,  
84 upwelling, and low-oxygen upwelling waters ([Fig. 1a](#)). Vertically-integrated backscatter of acoustic  
85 profiles—a proxy of pelagic biomass—was minimum in subpolar and oligotrophic-gyre waters, moderate  
86 in subtropical waters, and higher in rich temperate and upwelling waters, including those in oxygen  
87 minimum zones ([Fig. 1b-m](#)). With the exception of subpolar waters, this distribution was consistent with  
88 patterns of pelagic biomass worldwide, according to net-sampling studies<sup>25,36</sup>. The most distinctive feature  
89 in the classification was the shape of acoustic profiles, which illustrated the vertical structure of marine life  
90 across oceanic systems. While subpolar profiles were characterized by a smooth depth-increasing  
91 backscatter signal ([Fig. 1b,c](#)), those in rich upwelling and low-oxygen areas presented prominent peaks in



92 epipelagic and mesopelagic waters (Fig. 1j-m). These peaks denoted the presence of strong sound-  
93 scattering layers, which were also present—albeit with lower intensity and deeper depths—in gyre,  
94 subtropical and temperate systems (Fig. 1d-i). The classification also showed the main factors modulating  
95 the distribution of sound-scattering layers at global-scale. First, increased light penetration in oligotrophic  
96 ocean-gyre areas push mesopelagic fauna to deep waters<sup>37</sup>, while in productive systems, the presence of  
97 subsurface oxygen minimum zones constrains organisms to thinner layers near the surface<sup>38,39</sup>. Second, the  
98 intensity of these animal layers is expected to be higher in productive oceanic areas such as temperate,  
99 upwelling, and low-oxygen-upwelling systems<sup>31</sup>, as shown by our classification. The differences between  
100 day and night profiles—in particular the exchange of backscatter maxima between epipelagic and  
101 mesopelagic waters—illustrates that diel vertical migration is more intense in productive areas. In principle,  
102 the integrated backscatter of profiles was expected to be higher at night due to the incorporation of migrants  
103 from waters below our sampling range, however, that was not the case for upwelling and low-oxygen  
104 regions (Fig. 1j-m). While vertical migration itself is the main source of day and night differences in water-  
105 column backscatter, changes in the swimbladder condition of fish during these excursions are also known to  
106 have important effects on how sound is reflected back to surface<sup>40</sup>. Additionally, part of the night  
107 backscatter signal of migrants might be hidden above our sampling depth range. Due to this diel variation  
108 of backscatter, we ultimately used day and night acoustic estimates as complementary indicators of pelagic  
109 biomass in the remainder of this study. Both indicators together provided a more complete view of the  
110 global variation of biomass, by including the two possible backscattering scenarios in the water column.

111 **Present-day global seascape.** We tested ten supervised learning algorithms, as well as ten potential  
112 environmental predictors, to extend our seascape classification beyond the observation locations. Cross-  
113 validation tests and recursive elimination of weak predictors revealed that the best performance was  
114 achieved with a random forest classifier trained with satellite-derived chlorophyll concentration, subsurface  
115 dissolved oxygen, and sea surface temperature (78% predictive accuracy, see model selection and  
116 performance assessment in [Methods](#) and [Extended Data Figs. 4-6](#)). We extended the classification with this  
117 model at global scale, using the mean environmental conditions for the period 2000-2020. Seascape classes  
118 were coherently distributed along large-scale oceanographic systems associated with subpolar, gyre,  
119 subtropical, temperate, upwelling, and low-oxygen upwelling waters (Fig. 2a). As this partitioning relied on  
120 the combined day and night structure of acoustic profiles, their boundaries reflected not only differences in  
121 water-column biomass but in qualitative community properties such as the vertical distribution or the  
122 migration patterns of pelagic fauna. Indeed, net-based studies on the distribution of mesopelagic fish—  
123 likely the major contributor to backscatter<sup>41</sup>—show comparable community transitions between ocean-  
124 gyre, equatorial, coastal-boundary, and mid-latitude temperate systems<sup>25,26,42</sup>. Regionalisations based on

125 broader pelagic fauna inventories also identified fairly similar oceanographic biomes<sup>43–45</sup>. We therefore  
126 consider these acoustic seascape classes as “echobiomes”, as they represent sound-scattering communities  
127 with comparable structural and functional properties but not necessarily geographically connected or  
128 sharing the same species composition<sup>44</sup>. The vertical integral of the acoustic profiles predicted by our  
129 model can also be regarded as an indicator of pelagic biomass around the globe (Fig. 2b). Day and night  
130 biomass proxies presented similar spatial patterns, with minimum values in ocean-gyre and subpolar  
131 systems, and maximum in equatorial, temperate, and coastal-boundary systems (see night projections in  
132 Supplementary Fig. 1). Differences between low and high backscatter areas were however larger when  
133 using daytime data. These extended global projections were also consistent with large-scale biomass charts  
134 derived from net sampling<sup>25,36</sup>. The only exception occurred in subpolar echobiomes, where net based  
135 estimates were not as low in comparison to other regions<sup>25,36</sup>.

136 **Future global seascape.** Future changes in the distribution of echobiomes were then calculated by  
137 rerunning our model with average environmental conditions projected for 2080-2100. These were initially  
138 obtained from simulations of 13 different CMIP6 climate models forced by the “business-as-usual” high-  
139 emission scenario SSP5-8.5 (see Methods). Our results point to a massive redistribution of the acoustic  
140 seascape by the end of the 21<sup>st</sup> century, largely driven by the expansion of low-productive ocean-gyre and  
141 subtropical echobiomes towards current equatorial, temperate, and coastal-boundary rich systems (Fig. 2c-  
142 e). Overall, this rearrangement of the seascape would modify 20% of the total ocean surface analysed in  
143 comparison to present-time values (Fig. 3e). The expansion of ocean-gyres against surrounding systems is  
144 expected to promote a generalized biomass decline between 40°S and 40°N, while the poleward migration  
145 of temperate systems would result in biomass gains at higher latitudes. These regional biomass changes  
146 could locally reach up to 40% (Fig. 2f). According to our projections, biomass changes will be significant  
147 and consistent across latitudes and ocean basins, for most climate forcings considered, and regardless of  
148 whether day or night backscatter is used as proxy of biomass (Fig. 3a). Considering the day backscatter  
149 biomass proxy, expected biomass losses from 40°S and 40°N would range between 3 and 22%, with major  
150 losses in the tropics. Biomass gains at subpolar latitudes would range between 9 and 16% in the northern  
151 hemisphere, and between 8 and 31% in the southern hemisphere (Fig. 3a). Despite the opposing changes  
152 between low and high latitudes, projected losses would far outweigh projected gains as the ocean’s surface  
153 between 40°S and 40°N represent 70% of the total. The picture was qualitatively similar when the night  
154 backscatter proxy is considered, but the magnitude of biomass change would be lower (see Fig. 3a and  
155 Supplementary Tables 2 and 3). Both day and night biomass changes were largely driven by mesopelagic  
156 fauna and, to a lesser extent, by migratory epipelagic fauna at night (see Supplementary Fig. 1). Further, the  
157 displacement of echobiomes is expected to affect the vertical distribution of biomass around the globe. The

158 most significant and consistent change would take place in tropical upwelling regions, where epipelagic  
159 and mesopelagic fauna is expected to deepen from 10 to 100 meters. This process would result from an  
160 expansion of the deep sound-scattering fauna, currently in warm low-productive regions, into tropical  
161 upwelling systems (see [Supplementary Fig. 2](#)).

162 **Likely future.** Mid-trophic level fauna projections presented above are based on changes in environmental  
163 conditions projected by the average of the latest generation of Earth system models, CMIP6, and  
164 considering the high carbon emission scenario SSP5-8.5. While CMIP6 is the current baseline for climate-  
165 based socioeconomic and ecosystem assessments<sup>46</sup>, comparative studies with the previous generation of  
166 climate models indicate that CMIP6 projects stronger warming but weaker and less consistent declines in  
167 primary production than CMIP5<sup>13,14</sup>. This raises the question of the sensitivity of our projections under such  
168 differences in climate forcing. To address this, we extended our analysis and forced our projections with a  
169 wide variety of CMIP5 and CMIP6 individual model outputs, under equivalent high carbon emission  
170 scenarios, RCP8.5 and SSP5-8.5 (see [Supplementary Figs. 3-10](#)). The most significant finding of this  
171 intercomparison was that 19 out of 20 different climate forcings provided results consistent with the  
172 average CMIP6 projection shown here. Virtually, all future oceans projected by Earth system models over  
173 the last decade produce the same outcome: biomass losses in low and mid-latitudes and gains in subpolar  
174 ecosystems. In fact, our model projects very similar average biomass changes across latitudes when forced  
175 by CMIP5 or CMIP6 average environmental conditions (maximum median differences of 3 percentage  
176 points, see [Fig. 3b](#)). However, larger differences across CMIP6 simulations resulted in more uncertain  
177 biomass change projections. We further conducted an assessment on how environmental drivers would  
178 affect mid-trophic level fauna if they acted separately. Such analysis showed that the major source of  
179 uncertainty in CMIP6-forced biomass projections comes from chlorophyll. It also shows that biomass  
180 losses in tropical and subtropical zones would be primarily driven by a combination of warming and  
181 chlorophyll decline, while biomass gains at higher latitudes would be fundamentally promoted by warming  
182 ([Fig. 3c](#)). This contrasting response of mid-trophic level fauna is explained by the different primary  
183 production regimes that comes along with warming in low and high latitude systems. Warming is assumed  
184 to increase metabolic rates such as feeding, respiration, or growth<sup>20</sup>. In a food-limited scenario, as indicated  
185 by our low-chlorophyll projections in tropical and subtropical waters, this would promote a decline in the  
186 consumer biomass stock<sup>47</sup>. On the other hand, warming where primary production is not limiting would  
187 promote species expansions, growth and reproduction, as it has been already observed in temperate-polar  
188 transitions zones affected by ocean warming<sup>48,49</sup>. Temperature and chlorophyll persist as the major drivers  
189 of biomass change in both CMIP5 and CMIP6 projections ([Extended Data Figs. 7 and 8](#)), but most

190 importantly, these changes would still take place even if only warming occurred, the most likely and  
191 unequivocal ocean change projected by Earth system models<sup>13,14</sup>.

192 **Alternative future.** We additionally projected biomass changes of mid-trophic level fauna, forced by  
193 CMIP6 environmental conditions in 2080-2100 under the low-emission scenario SSP1-2.6 (Fig. 3d). That  
194 is, if nations achieved strong mitigation measures to keep global warming below 2°C<sup>14</sup>. Our results show  
195 that such measures would largely halt the redistribution of echobiomes in comparison to the high-emission  
196 scenario. The contraction of echobiomes in upwelling and subpolar regions would be strongly mitigated,  
197 while oligotrophic gyres would remain virtually unaffected (Extended Data Figs. 9-10). In terms of  
198 biomass, these strong mitigation measures would contain changes below 10% in virtually all climate zones,  
199 and near zero in temperate systems (Fig. 3d). According to our calculations, all biomass changes projected  
200 under the CMIP6 low-emission scenario, either positive or negative, would be mitigated by 4 to 11  
201 percentage points with respect to the high-emission scenario. This implies that the impact will drop by at  
202 least two thirds at all latitudes. Similar mitigation rates were estimated under CMIP5 forcing or when using  
203 night backscatter as proxy of biomass (impact reductions from 3 to 13 percentage points, see  
204 Supplementary Tables 2 and 3).

205 **Interpreting climate-forced acoustic-based projections.** Our projected biomass changes are consistent  
206 with virtually all marine ecosystem models under comparable climate change scenarios, both in magnitude  
207 and direction<sup>16-19</sup>, reconciling acoustic-based and ecosystem model projections for the first time<sup>34</sup>. The way  
208 our model works stands out for its simplicity. Understanding species physiology or ecological interactions  
209 is not required to determine their response to ocean warming and shifts in primary production. This is often  
210 a difficult task in the implementation of ecosystem models and a major source of uncertainty in marine  
211 fauna projections<sup>15,20</sup>. Our approach simply links sonar observations of sound-scattering fauna with current  
212 environmental conditions and projects the future distribution of this fauna under new conditions. As such, it  
213 assumes that current echobiomes will follow their environmental niches. This assumption, which is  
214 ecologically coherent, has further been corroborated by studies that already detected large-scale shifts in the  
215 distribution of multiple species following new thermal niches due to ocean warming<sup>48,49</sup>. Yet, as any  
216 observational approach, our method presents limitations that must be taken into consideration.  
217 Echosounders detect organisms that are efficient sound reflectors at certain frequencies according to their  
218 physical properties. For instance, the frequency used here, 38 kHz, is known to maximize the signal of gas-  
219 bearing organisms such as small mesopelagic fish or siphonophores<sup>50</sup>. Weaker fluid-like organism might  
220 hence be under-represented and this should be taken into consideration when comparing our results with  
221 more specific fauna compartments from ecosystem models. In relation to this issue, the acoustic signal in  
222 subpolar echobiomes was the only one that misrepresented pelagic biomass charts elaborated with fishing

223 gears<sup>25,36</sup>. It is unlikely that rich subpolar systems host less animal biomass than low-productive ocean  
224 gyres. We therefore believe that the subpolar decay of signal observed is related to documented latitudinal  
225 changes in the backscatter-to-biomass ratio<sup>51</sup>, and due to the reduction of gas-bearing organisms in subpolar  
226 systems<sup>52-54</sup>. Because of this, the expansion of rich temperate echobiomes over subpolar echobiomes might  
227 amplify our projected biomass gains at high latitudes. We attribute therefore a greater uncertainty to  
228 biomass change projections in subpolar waters, not only for the aforementioned reasons, but also because  
229 this echobiome lacked observations in the North hemisphere. Future assessments will therefore require to  
230 investigate on basin-scale acoustic properties of pelagic fauna, and increase observations at high latitudes,  
231 including the Arctic. Another limitation relates to the model's inability to predict new echobiomes in  
232 regions where projected environmental changes have no analog with historical observations. New climate  
233 will emerge in tropical waters, where existing species are expected to reduce in size and biomass due to  
234 extreme warming and low productivity conditions<sup>55</sup>. As these processes are not captured, this might  
235 constitute another source of underestimation in our projected declines of ocean fauna. Finally, our  
236 projections, as any other, inherit the uncertainties of climate simulations<sup>13,14</sup>. Our results should then be  
237 revisited under future simulation exercises, especially those projecting primary production and low trophic  
238 level compartments, as they currently represent the largest source of uncertainty in mid-trophic level fauna  
239 projections<sup>14,19</sup>.

240 **Concluding remarks.** We use the last-generation of Earth system models, CMIP5 and CMIP6, along with  
241 sonar observations, to project the future distribution of ocean fauna under multiple scenarios of climate  
242 change. As such, this study constitutes a ground-truth reference for ecosystem model simulations and  
243 provides an alternative empirical approximation to envisage and anticipate the effects of climate change  
244 with greater confidence.<sup>20</sup> Our results indicate that ocean warming and shifts in primary production will  
245 result in 1) substantial reorganization of biogeographical provinces, 2) significant reductions of mid-trophic  
246 level fauna in low and mid latitude systems, and 3) massive expansion of temperate species towards high-  
247 latitude systems. Nearly 70% of the global ocean is projected to lose animal biomass. Such loss is  
248 expected to bring food insecurity worldwide<sup>56</sup> and declines of carbon export mediated by vertical migration  
249 or the sinking of matter produced by animals<sup>57</sup>. Mid-trophic level fauna may hence constitute a new  
250 feedback loop component in the global climate system which may accelerate the risks and time horizons  
251 projected by the IPCC<sup>46</sup>. We further show that strong mitigation measures to contain global warming below  
252 2°C would reduce our projected biomass changes by at least two thirds in comparison to the high-emission  
253 scenario. Paradoxically, now that ambitious actions need to be taken to halt the worst effects of climate  
254 change, mesopelagic fish, likely the largest unexploited stock of mid-trophic level fauna worldwide<sup>31</sup>, is in  
255 the spotlight of the fishing industry<sup>58,59</sup>. Based on these results, we call for caution in managing this

256 fundamental component of pelagic ecosystems and urge to place mid-trophic level fauna at the very centre  
257 of global climate policies and research.

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267 **Author contributions.** A.A., A.B., M.L., C.M., and A.L.D designed the study. M.L. and T.G. processed  
268 environmental data. J.H. and M.G. processed acoustic data. A.A. analysed environmental and acoustic data  
269 and wrote the manuscript with contribution from all authors.

270 **Competing interests.** The authors declare no competing interests.



## Figure legends

271 **Figure 1: Acoustic seascape classification.** **a**, The shape of day and night acoustic profiles was used to classify the ocean seascape through  
272 hierarchical clustering. **b-m**, Day and night profiles for each seascape class are shown in top and bottom panels, respectively. Central and side  
273 curves represent the median and interquartile range (Sv, dB re  $m^{-1}$ ). The vertical integration of these curves—a proxy for pelagic biomass—is  
274 indicated in grey at the bottom of each profile (nautical area scattering coefficient,  $m^2 nmi^{-2}$ ). Colours indicate the acoustic seascapes identified,  
275 which were associated to subpolar (brown), ocean-gyre (olive), subtropical (cyan), temperate (orange), upwelling (red), and low-oxygen  
276 upwelling (purple) waters.

277  
278 **Figure 2: Biogeography and acoustic-based biomass.** Distribution of subpolar (SP), gyre (G), subtropical (ST), temperate (T), upwelling  
279 (UW), and low-oxygen (LO) echobiomes and daytime water column backscatter ( $m^2 nmi^{-2}$ ) as a proxy of animal biomass. Results are shown  
280 for 2000-2020 in **a** and **b**, for 2080-2100 projections in **c** and **d**, and as the present-to-future change between these two periods in **e** and **f**.  
281 Biogeographic change in **e** is represented with light and bold colour shades, indicating the present distribution and future expansion of  
282 echobiomes, respectively. Backscatter change in **f** is indicated as percentage, relative to present-time values. Future projections are forced by  
283 the average climate outputs from 13 CMIP6 Earth system models. Contour dashed and continuous lines indicate areas where the standard  
284 deviation of projected changes exceeded values of 15 and 20, respectively.

285  
286 **Figure 3: Biomass changes by 2080-2100 under variable climate forcing.** **a**, Day (red) and night (black) biomass projected latitudinal  
287 changes forced by CMIP6 climate projections under high-emission scenario. **b**, Day biomass forced by CMIP6 (red) and CMIP5 (black)  
288 climate projections under high-emission scenario. **c**, Day biomass projected changes forced by CMIP6 climate projections under high-emission  
289 scenario if sea surface temperature (SST, pink), subsurface dissolved oxygen (SDO, blue), or chlorophyll (CHL, green) projected  
290 environmental drivers occurred in isolation. **d**, Day biomass projected changes forced by CMIP6 under high (red) and low (black) emission  
291 scenarios. **e**, Percentage of the global ocean's area for each latitudinal range. Fixed and changing features of biomass projections are indicated  
292 at the top and at the bottom of each panel, respectively. Boxes show the median and the interquartile range while whiskers indicate the 5-95%  
293 percentile range. They represent the spread of biomass changes due to different climate forcing (7 CMIP5 or 13 CMIP6 climate forcings). Low  
294 and high emissions respectively designate SSP5-8.5 and SSP1-2.6 IPCC greenhouse emission scenarios.

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## 295 **Methods**

296 **Data collection and processing.** Georeferenced single-beam acoustic data at 38 kHz, spanning from 2001  
297 to 2020, was collated from public databases, sourced by Australian, British, French, Peruvian and Spanish  
298 research programs in the Pacific, Atlantic and Indian Oceans ([Supplementary Table 1](#)). Most of data were  
299 already available as quality-controlled, calibrated processed data, with the exception of the Malaspina  
300 circumnavigation expedition data, which were processed for this study following standard procedures. This  
301 processing included background noise correction<sup>60</sup>, automatic removal of corrupted signal<sup>61</sup>, manual  
302 cleaning of persistent corrupted signal and aliased seabed, and resampling to 10 m height and 1000 m wide  
303 data cells, using Matecho v6.7<sup>62</sup>. Acoustic profiles were required to present consistent depth range and  
304 resolution, and continuous water column signal, in order to be transformed into functional curves (see  
305 section below). We therefore limited all profiles to the common largest depth range available in the dataset,  
306 from 20 to 750 m depth, and they were interpolated to a consistent vertical resolution of 10 m. To ensure  
307 the continuity of the water column signal, we remove from the dataset any profile with either missing or  
308 extremely weak backscatter, the later likely introduced when cleaning low signal-to-noise regions<sup>60</sup>. The  
309 threshold below which a profile was considered to be altered by this pre-processing step was set to -130 dB,  
310 since no biological backscatter is expected below this level<sup>63</sup>. This threshold permitted to remove profiles  
311 where the continuity of the signal was compromised by noise conditions without the risk of removing  
312 backscatter from animals. Profiles where the seabed was above 1000 m depth were removed to exclude  
313 continental shelves from the analysis, and profiles where the sun was between 0° and 18° below the horizon  
314 were removed to avoid vertical migration events during dawn and dusk, following the astronomical  
315 definition of twilight. GPS time and position of profiles along with global bathymetry data<sup>64</sup> were used to  
316 estimate the solar azimuth angle and seabed at the time of data acquisition. Profiles that passed the filtering  
317 process (equivalent to more than 350,000 km around the globe, see [Supplementary Table 1](#)) were grouped  
318 and averaged into geographical cells of 4 degrees longitude and 4 degrees latitude. Only cells with at least  
319 10 km of acoustic data recorded were accepted to compute average profiles. This was done separately for  
320 day and night acoustic data, i.e, we generated two global datasets with day and night profiles. As the  
321 resulting averaged profiles might result from different sampling missions across the annual cycle, the  
322 monthly sampling effort for each averaged profile was recorded. This was used afterwards to correct the  
323 environmental inputs used for training the acoustic seascape predictive model (see below). In total, mean  
324 profiles were computed for 465 cells, which represented the 16% of the ocean surface ([Extended data Fig.](#)  
325 [1](#)).

326 **Functional data analysis.** Functional data analysis (FDA<sup>35</sup>) was used to describe and analyse the variation  
327 of the acoustic signal along the depth dimension. The analysis was implemented using the FDA module  
328 available in EchoPY v1.1<sup>65</sup>. This included turning the discretized data of profiles into functions and use the  
329 descriptors of these functions to explore the main modes of signal variation in the water column through  
330 functional principal components analysis (fPCA<sup>35</sup>). In the present study, each observation consisted of a  
331 4x4 cell with two variables: day and night Sv profiles. Each profile was decomposed into a sequence of 18  
332 basis functions (see [Extended Data Fig. 2](#)). We used cubic splines as the most suitable basis functions to  
333 represent non-periodic functional data<sup>66</sup>. With 18 basis functions from 20 to 750 m depth, each cubic spline  
334 was adjusted to the data every ~40 m. At ocean-basin scale, 38 kHz layers are usually 100 m wide or  
335 larger<sup>32</sup>, we therefore considered this resolution appropriate to outline the vertical structure of 38 kHz  
336 profiles without over-fitting. In a functional scenario, and for the application of fPCA, the counterparts of  
337 the Sv values are the function coefficients<sup>35</sup>, which were concatenated from day and night profiles. In total,  
338 36 coefficients (18+18) for each of the 465 geographical cells were used to build a cross-covariance matrix  
339 and find a suitable number of principal components (PCs) explaining most of the dataset variance ([Fig.](#)  
340 [Extended Data Fig. 2](#)). One of the most significant advantages of fPCA with respect to the conventional one  
341 is the possibility to access the variance contained within each principal component as a function of depth<sup>35</sup>.  
342 This allowed diagnosing the main modes of profile variance in the system ([Extended Data Fig. 3](#)),  
343 simultaneously during day and night. This was essential for later interpretation of the acoustic seascape  
344 classification. Further details on the implementation of fPCA can be found in Ramsay and Silverman  
345 (2005)<sup>35</sup>.

346 **Seascape classification.** Day-night profiles averaged for each geographical cell were classified using  
347 agglomerative hierarchical clustering from the scikit-learn Python module<sup>67</sup>. We used the function  
348 coefficients decomposed in 8 principal components (PCs) as descriptors for the classification, which  
349 accounted for more than 90% of the dataset variance. Agglomerative hierarchical clustering was chosen  
350 because it is suitable to classify globularly distributed data<sup>67</sup>, provides valuable information on the  
351 hierarchical similarity of profiles between clusters, and showed fairly consistent results in comparison with  
352 other classification tools (see [Extended Data Fig. 5](#)). The same first 8 PCs used in the classification were  
353 used to reconstruct the acoustic profiles, that is, keeping more than 90% of profile variance in the dataset  
354 ([Extended Data Fig. 3](#)). These profiles were then averaged for each acoustic seascape class (median and  
355 interquartile range, see [Fig. 1](#)).

356 **Future environmental conditions.** We initially analysed simulation outputs from 13 climate models  
357 extracted from the CMIP6 archive<sup>68</sup>. For each model, we use the first member of the historical experiments  
358 and the corresponding member of a low and high emission future scenario from the Shared

359 Socioeconomical Pathways (SSP), namely the SSP126 and SSP585. While the SSP585 scenario assumes  
360 accelerated globalization and rapid economic and social development of developing countries coupled with  
361 the exploitation of abundant fossil fuel resources, SSP126 is an optimistic scenario designed with the aim  
362 of simulating a development that is compatible with the 2°C target, assuming climate protection measures  
363 being taken. The model selection procedure was based on the availability of temperature, chlorophyll and  
364 oxygen data for the three experiments selected for a given model. Future mean anomalies for each of these  
365 models were calculated as the averaged annual difference between the 2080-2100 and the 1995–2014  
366 historical periods. All data were then compiled over the <sup>[[[]]]</sup> same 4° × 4° grid. For the sake of comparison  
367 with the previous CMIP exercise and based on the same selection procedure, we also analysed simulations  
368 outputs from 7 CMIP5<sup>69</sup> climate models: for each model, we used one member of the historical experiment  
369 and the corresponding member of the high emission scenario RCP85. The RCP 8.5 scenario has an identical  
370 radiative forcing level to SSP5-8.5 (i.e., 8.5 W m<sup>-2</sup> at 2100). Future mean anomalies for these models were  
371 calculated as the averaged annual difference between the 2080-2100 and the 1986-2005 periods.

372 **Seascape predictive model.** We used a machine learning approach trained with clustering results, in order  
373 to project the acoustic seascape beyond our observations<sup>70,71</sup>. A Random Forest learning algorithm was  
374 used to predict the acoustic profiles at global scale. This method was used among others after testing the  
375 prediction accuracy of up to 10 models from the Python Scikit-learn classifier module<sup>72</sup> by means of cross-  
376 validation analyses ([Extended Data Figs. 4-6](#)). The model was trained with sea surface temperature,  
377 subsurface dissolved oxygen (150-500 m depth), and chlorophyll as inputs, while acoustic seascape classes  
378 were used as the output. We used temperature and dissolved oxygen data from the 2018 World Ocean  
379 Atlas<sup>73,74</sup> and chlorophyll from the Ocean Colour Climate Change Initiative<sup>75</sup>. The data period chosen was  
380 between years 2000 and 2020 in order to encompass the time coverage of the acoustic dataset. A wider set  
381 of predictors were tested initially, such as temperature and dissolved oxygen at several depth intervals, the  
382 depth of mixed layer, or primary production. The optimal selection of predictors was decided using a  
383 backward elimination approach, starting with all candidate variables and recursively removing the one with  
384 less involvement in the classification result. In order of importance, subsurface oxygen, chlorophyll, and  
385 sea surface temperature were the variables that—combined—provided the best prediction accuracy during  
386 cross-validation tests. These tests were performed using a 75% of the acoustic classification as the training  
387 dataset and the remaining 25% for validating the results. The operation was repeated 100 times with  
388 random subsets for training and validation to obtain average prediction accuracy metrics (F1 score). Each  
389 time, a random shuffle operation was selected to improve randomization (see [Extended Data Fig. 4](#)). To  
390 overcome the problem of the uneven season coverage in the acoustic dataset, the model was trained with  
391 monthly-weighted environmental predictors for the period 2000-2020, based on the monthly sampling



392 effort of each acoustic profile in the dataset (see [Extended Data Fig. 1](#)). For instance, if the mean acoustic  
393 profile of a given geographical cell was computed with a sample of profiles biased to the summer season,  
394 temperature, dissolved oxygen, and chlorophyll predictors for training the model would be biased to the  
395 same direction. For that particular case, only mean summer environmental conditions for the period 2000-  
396 2020 would be used as predictors.

397 **Seascape and biomass projections.** Once the Random Forest classifier was trained, acoustic seascape  
398 classes were projected at global scale using mean environmental conditions of temperature, subsurface  
399 dissolved oxygen, and chlorophyll as inputs, for the periods 2000-2020 and 2080-2100. Contemporary  
400 environmental variables were obtained from the same sources as for training the model. For future  
401 variables, we computed historical-to-future mean anomalies from CMIP6 or CMIP5 Earth System model  
402 ensemble projections and we added these anomalies to contemporary environmental observations (see  
403 “Future environmental conditions” section). Our projections include day and night acoustic seascapes in the  
404 epipelagic and mesopelagic domains ([Supplementary Fig. 1](#)), global maps with the depth distribution of  
405 epipelagic and mesopelagic sound scattering ([Supplementary Fig. 2](#)), and vertically integrated backscatter  
406 maps, as an indicator of water-column biomass across multiple CMIP5 and CMIP6 Earth system models,  
407 and under both high-emission and strong-mitigation scenarios ([Fig. 2](#) and [Supplementary Fig. 3-10](#)). The  
408 Random Forest projection provided the probability of each acoustic seascape class to be allocated in a  
409 given location. The most voted ones were used to build the global acoustic seascape and the probabilities  
410 were used to compute weighed mean profiles for these locations, using the profiles of each acoustic  
411 seascape class (see [Fig. 1](#)). The backscatter of these projected profiles was vertically integrated and used as  
412 a metric of animal biomass in the water column. To provide measures of uncertainty due to multiple climate  
413 forcing, this biomass proxy was computed with backscatter projections forced by all the environmental  
414 outputs within the CMIP6 (n=13) and CMIP5 (n=7) Earth system model ensembles ([Supplementary Figs.](#)  
415 [3-10](#)). Median and percentile ranges (25<sup>th</sup>-75<sup>th</sup> and 5<sup>th</sup>-95<sup>th</sup> ) were provided from these computations (see  
416 [Fig. 3](#) and [Supplementary Tables 2 and 3](#)).

417



## 418 **Data availability**

419 All data used in the present study are publicly available. Acoustic data can be accessed through diverse  
420 internet repositories indicated in the [Supplementary Table 1](#). Observations of sea surface temperature and  
421 dissolved oxygen are available in the 2018 World Ocean Atlas ([https://www.ncei.noaa.gov/products/world-](https://www.ncei.noaa.gov/products/world-ocean-atlas)  
422 [ocean-atlas](https://www.ncei.noaa.gov/products/world-ocean-atlas)), and satellite chlorophyll observations can be accessed through the Ocean Climate Change  
423 Initiative data portal (<http://www.esa-oceancolour-cci.org>). CMIP5 and CMIP6 simulations are publicly  
424 available in the Earth System Grid Federation data portal (<https://esgf-node.llnl.gov>). We also provide in  
425 supplementary data the global acoustic atlases elaborated for the present study.

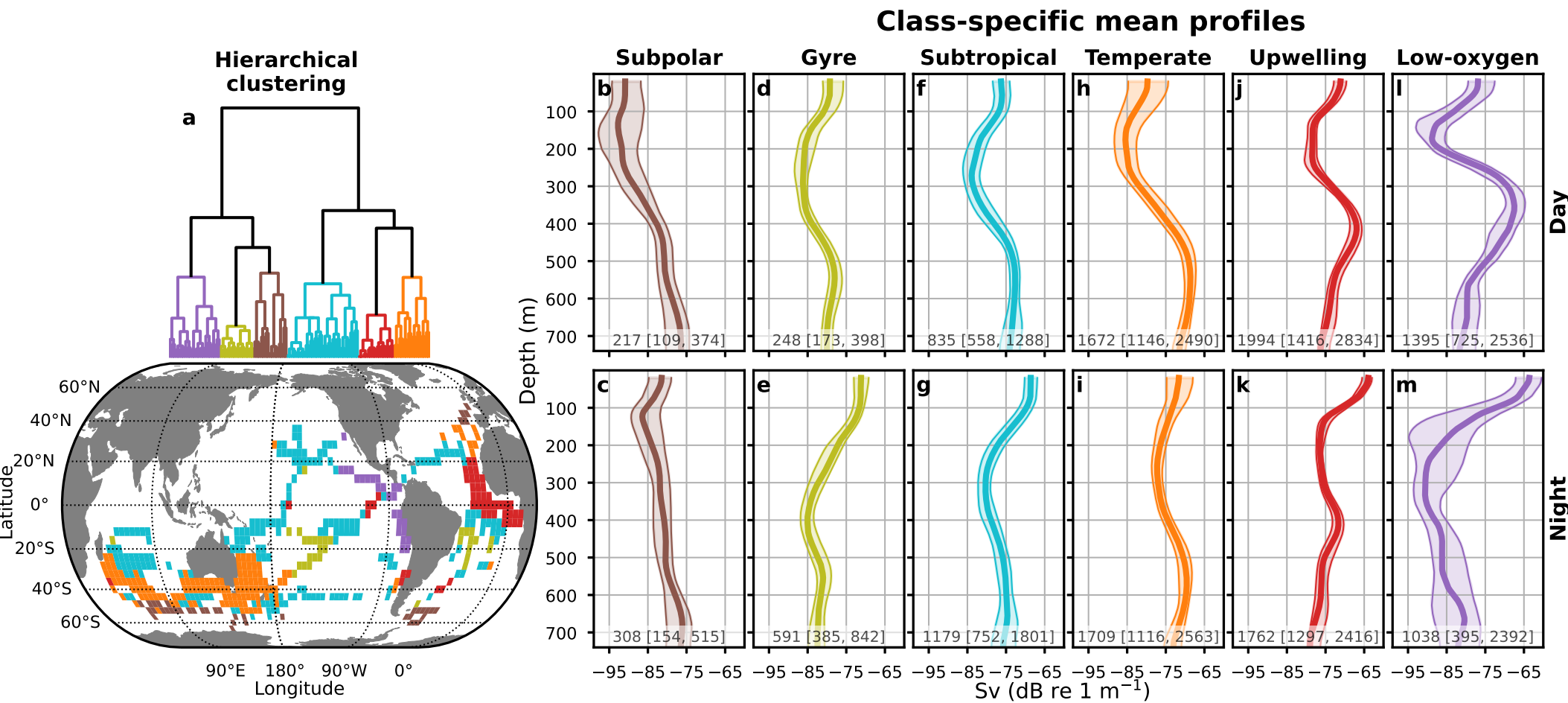
## 426 **Code availability**

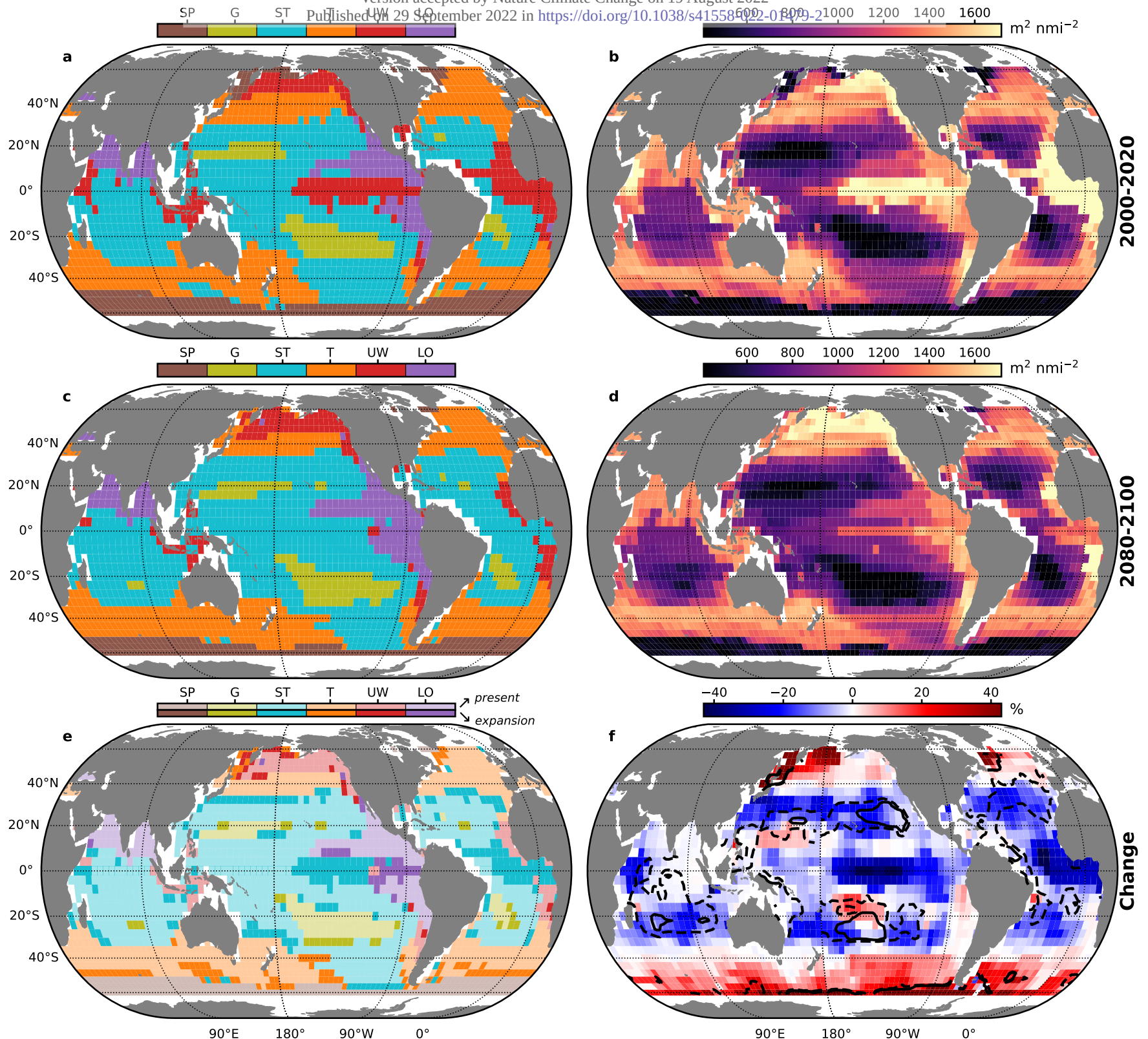
427 Raw acoustic data from the Malaspina circumnavigation expedition were processed using the open-source  
428 software Matecho v6.7, following the standard procedures detailed in Methods. The rest of acoustic  
429 repositories were already available as processed data. Data analysis was conducted with custom-made  
430 analysis routines in Python v3.8 and diverse open-source Python packages indicated in Methods. All  
431 analysis routines used in the present study are available upon request.

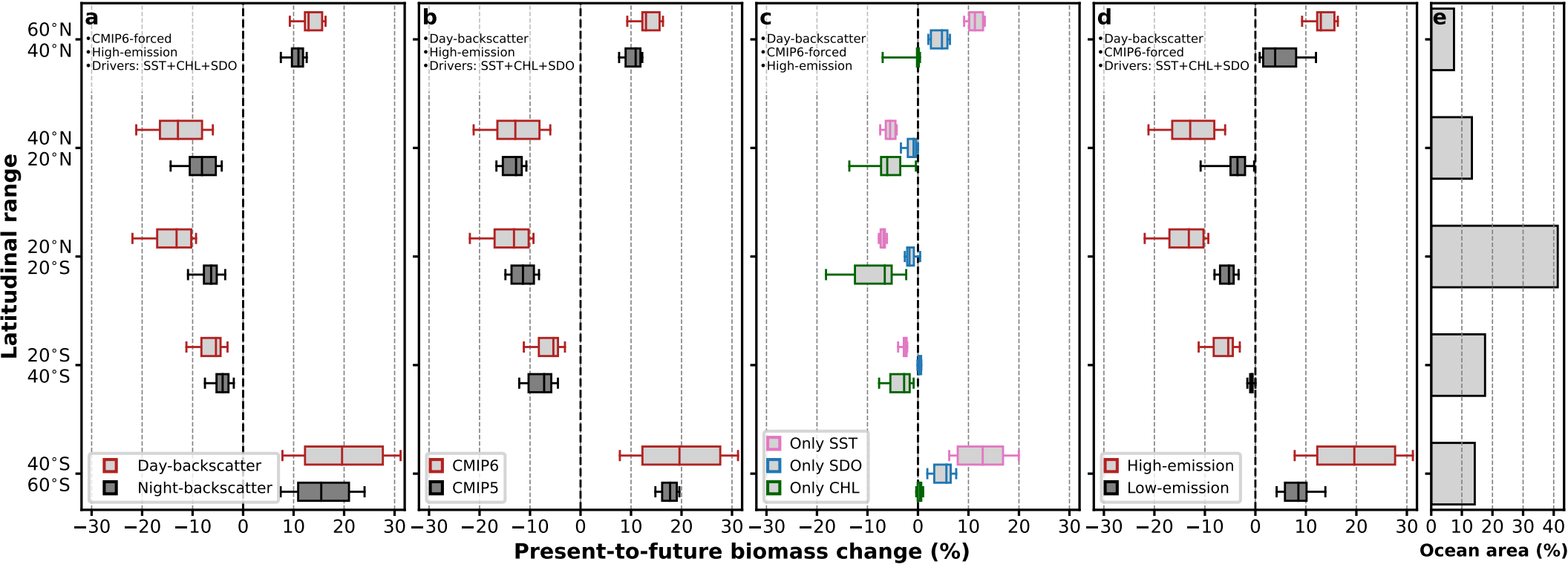
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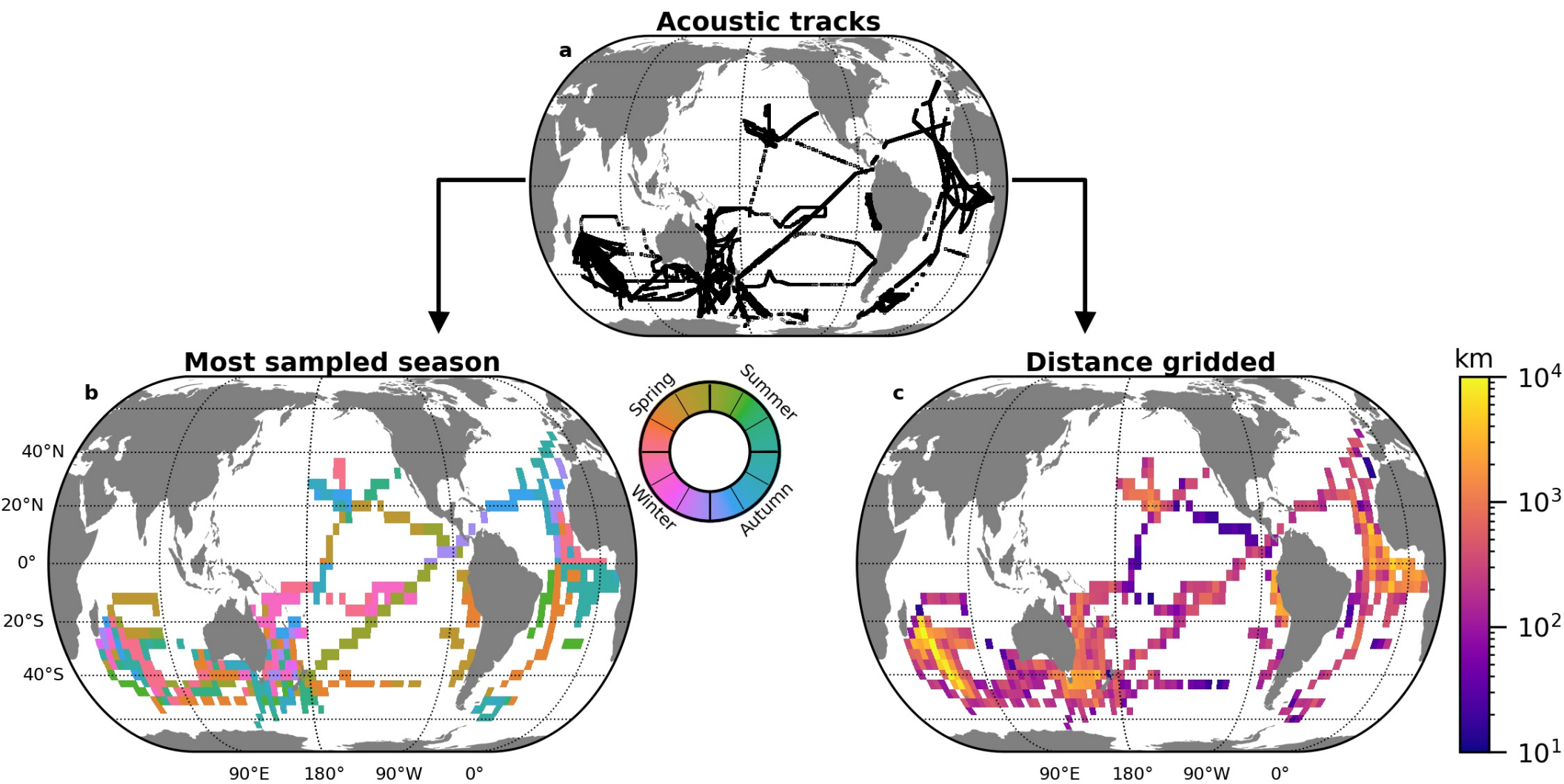
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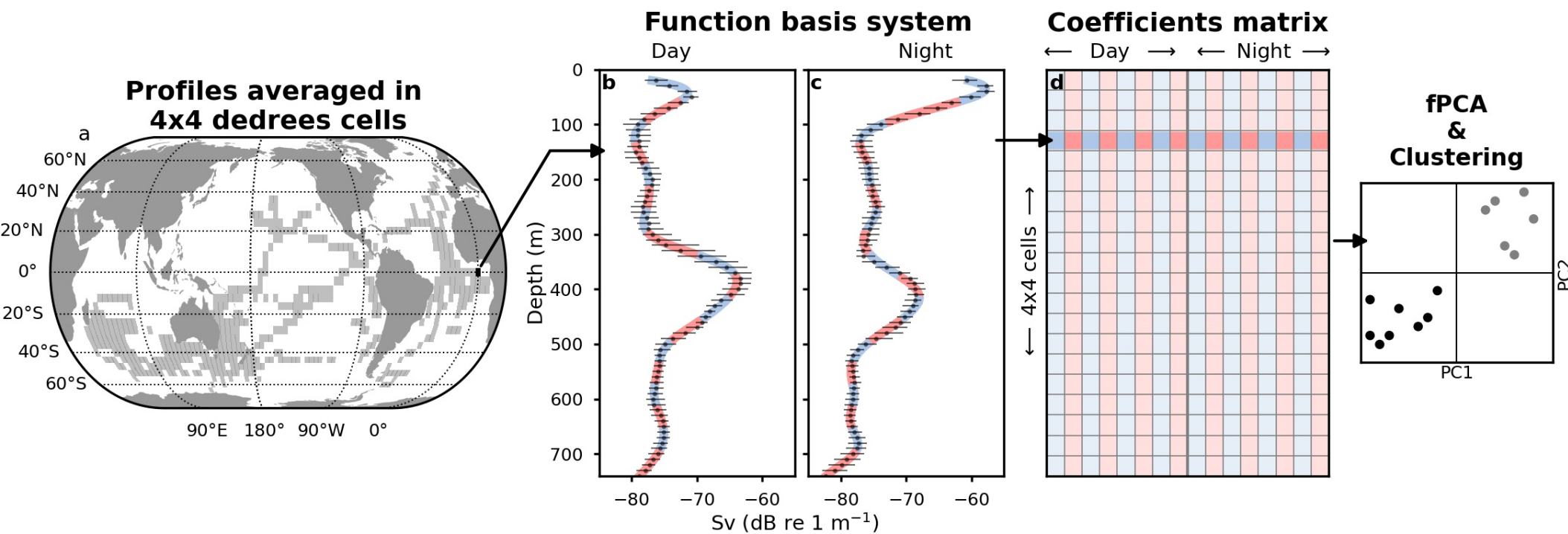




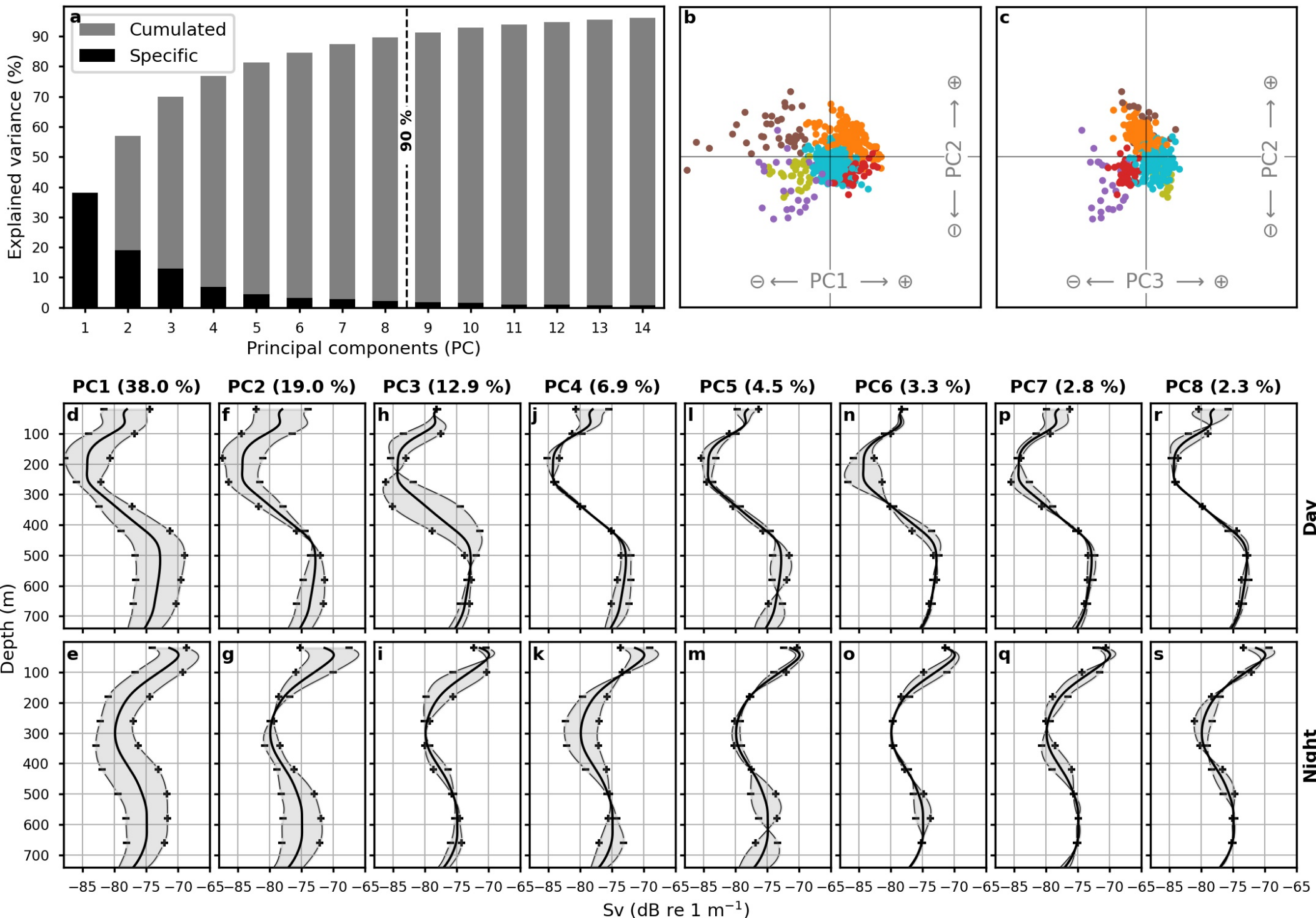






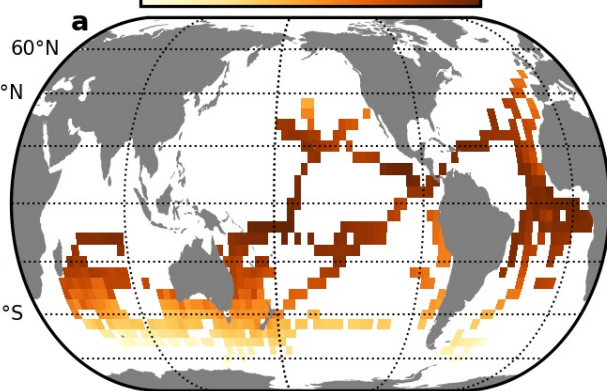






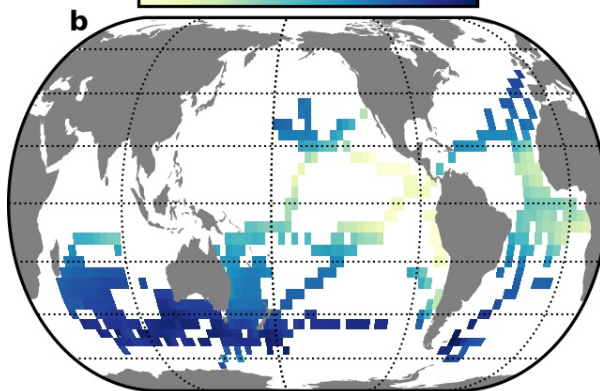
**Sea surface Temperature  
(SST, °C)**

10 20



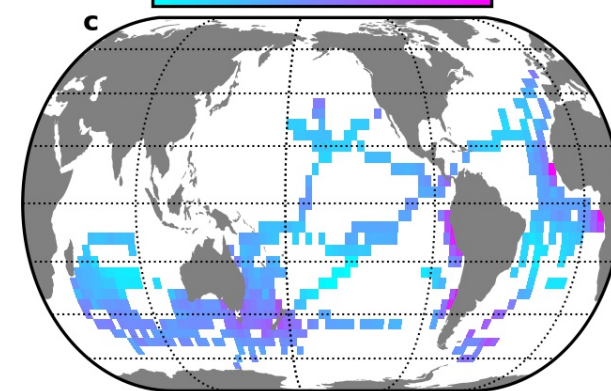
**Subsurface dissolved Oxygen  
(SDO, mmol kg<sup>-1</sup>)**

100 200



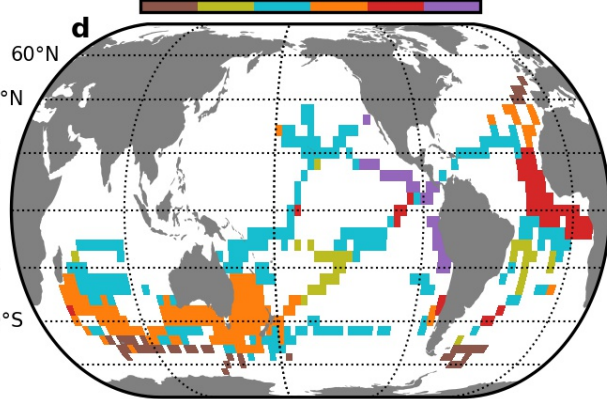
**Chlorophyll  
(CHL, mg m<sup>-3</sup>)**

10<sup>-1</sup> 10<sup>0</sup>



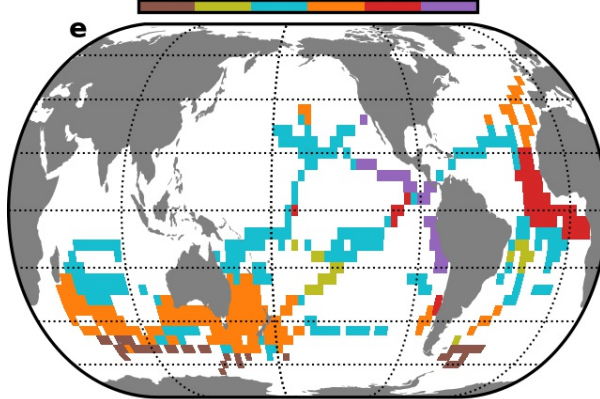
**Observed classification**

SP G ST T UW LO

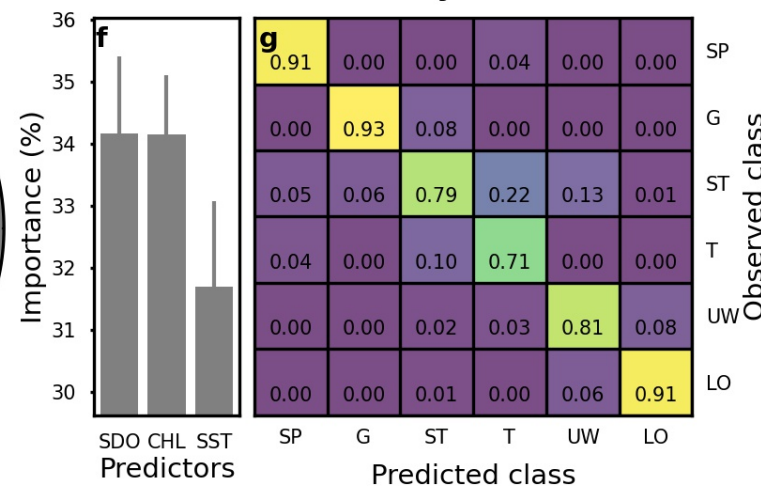


**Predicted classification**

SP G ST T UW LO

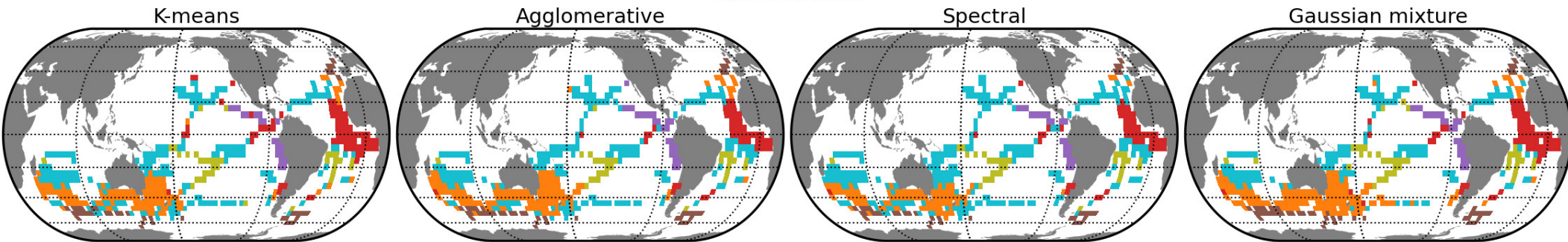


**Prediction accuracy: 0.78±0.04**





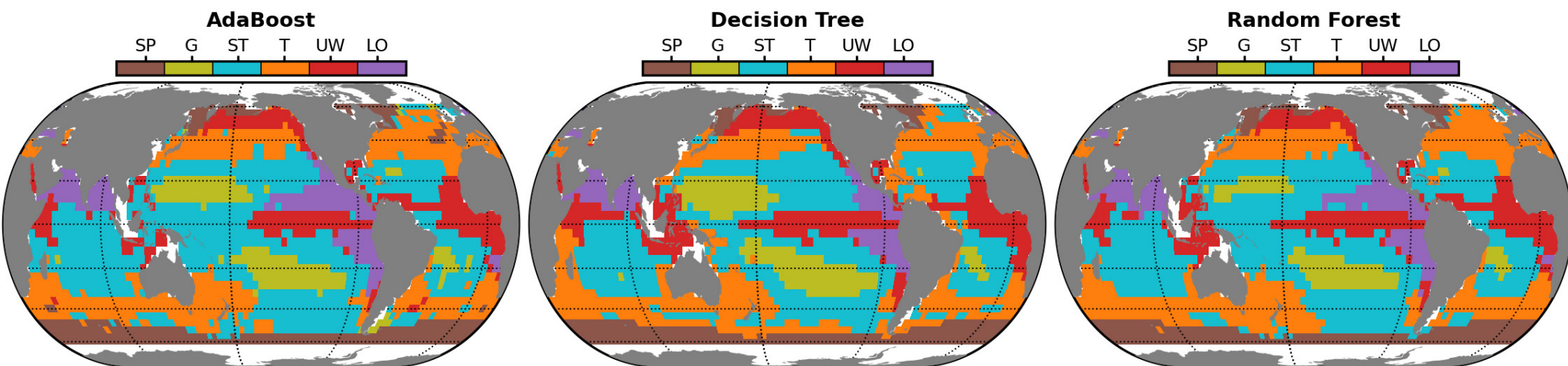
### Classifiers



### Prediction accuracy of global projections with 10 machine-learning algorithms

AdaBoost	Decision Tree	Gaussian Process	Naive Bayes	Nearest Neighbors	Neural Network	QDA	SVM-linear	SVM-RBF	Random Forest
0.76±0.03	0.75±0.03	0.60±0.03	0.63±0.03	0.62±0.02	0.69±0.04	0.59±0.06	0.61±0.04	0.66±0.03	0.78±0.04

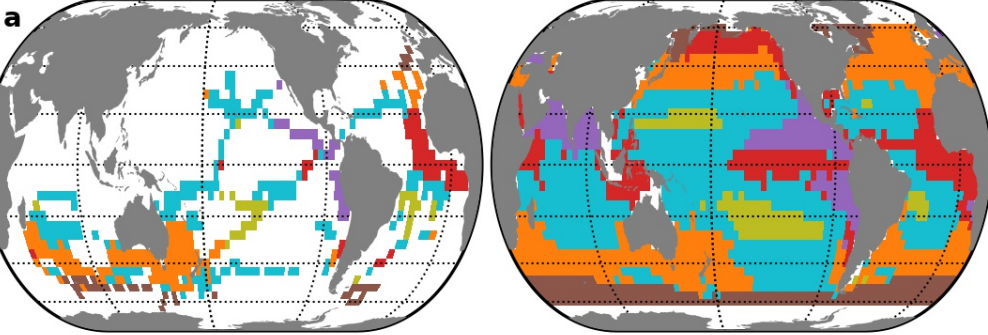
### 3-best projections



### Complete

Classification

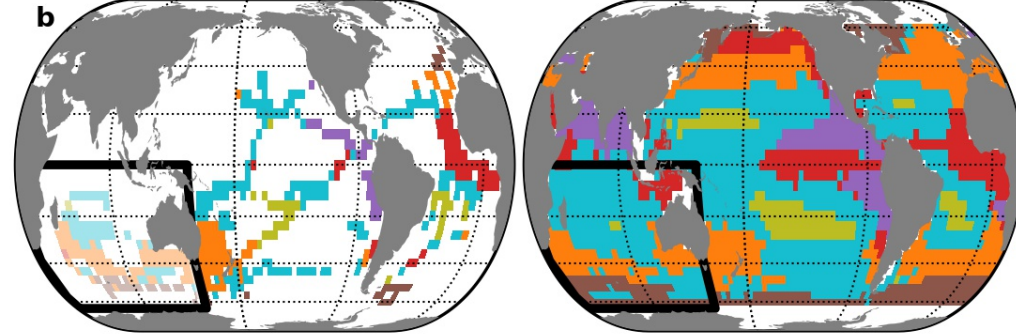
Prediction



### South Indian removed

Classification

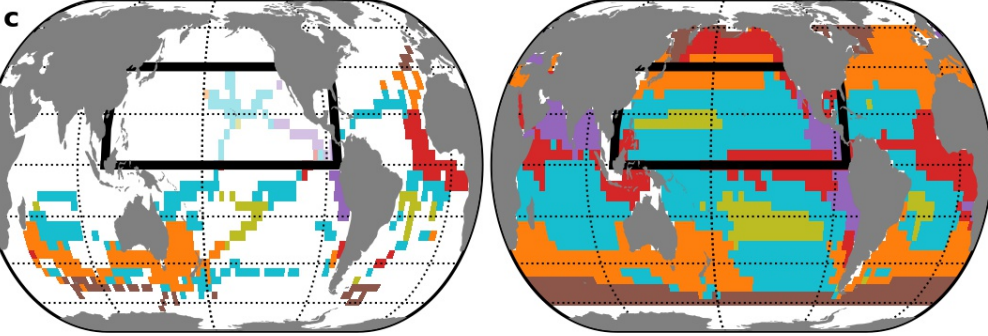
Prediction



### North Pacific removed

Classification

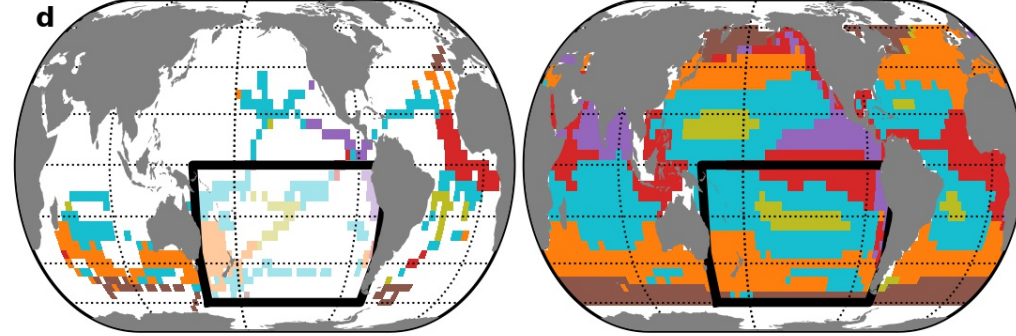
Prediction



### South Pacific removed

Classification

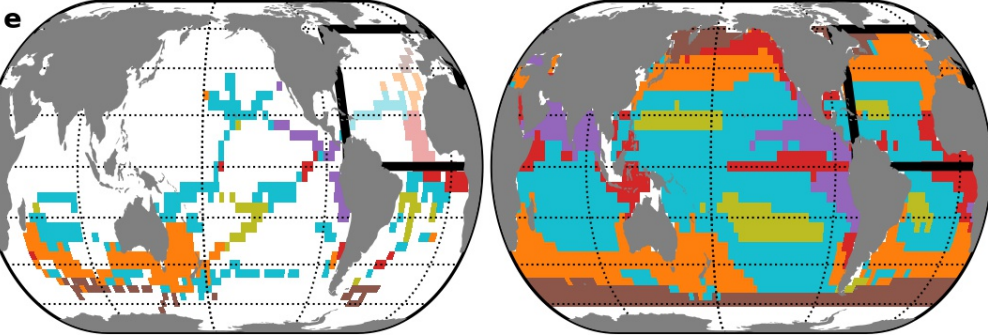
Prediction



### North Atlantic removed

Classification

Prediction



### South Atlantic removed

Classification

Prediction

