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# Prediction of unprecedented biological shifts in the global ocean

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31 **Abstract**

32 **Impermanence is an ecological principle<sup>1</sup> involving changes that can sometimes occur non-linearly**  
33 **as Abrupt Community Shifts (ACSs) to transform ecosystem states and the goods and services they**  
34 **provide<sup>2</sup>. Here, we present a model based on niche theory<sup>3</sup> to explain and predict ACSs at the global**  
35 **scale. We test our model using 14 multi-decadal time series of marine metazoans from zooplankton**  
36 **to fish, spanning all latitudes and the shelf to the open ocean. Predicted and observed fluctuations**  
37 **correspond, with both identifying ACSs at the end of the 1980s<sup>4-7</sup> and 1990s<sup>5,8</sup>. We show that these**  
38 **ACSs coincide with changes in climate that alter local thermal regimes, which in turn interact with**  
39 **the thermal niche of species to trigger long-term and sometimes abrupt shifts at the community**  
40 **level. A large-scale ACS is predicted after 2014 - unprecedented in magnitude and extent - coinciding**  
41 **with a strong El Niño event and major shifts in Northern Hemisphere climate. Our results underline**  
42 **the sensitivity of the Arctic Ocean, where unprecedented melting may reorganize biological**  
43 **communities<sup>5,9</sup> and suggest an increase in the size and consequences of ACS events in a warming**  
44 **world.**

45

46 **Main text**

47 The processes that cause long-term changes and Abrupt Community Shifts (ACSs) in ecosystems are  
48 poorly understood despite decades of research<sup>2,4,10-12</sup>. We define an ACS as a stepwise shift in  
49 community structure<sup>12</sup>, a definition that does not necessarily imply the existence of stable states<sup>2,10</sup>,  
50 which are rarely observed in pelagic ecosystems<sup>10,12-14</sup>. Such ACSs correspond to rapid and major  
51 alterations in species composition<sup>15</sup>, which alter biodiversity with consequences for ecosystem  
52 services. Here, we apply a framework based on the MacroEcological Theory on the Arrangement of  
53 Life (METAL; Methods and Supplementary Table 1 for a list of acronyms)<sup>12,16-18</sup>. METAL integrates key  
54 ecological concepts (e.g. the ecological niche *sensu* Hutchinson) into a unique and coherent scheme  
55 that unifies space and time patterns at both species and community levels and enables quantifiable  
56 predictions. METAL has been used to explain responses of species and communities to climate change  
57 and the large-scale arrangement of biodiversity<sup>12,16-18</sup>.

58

59 We applied the METAL-based model to investigate long-term community changes and ACSs in pelagic  
60 marine metazoans in the global ocean from 1960 to 2015. In each geographical cell of a gridded ocean,  
61 we built pseudo-communities from a pool of pseudo-species, i.e. simulated species characterised by  
62 unique thermal niches ranging from stenotherms (species with narrow temperature tolerance) to  
63 eurytherms (adapted to extreme temperature variations) and from psychrophiles (adapted to cold  
64 temperatures) to thermophiles (adapted to warm temperatures)<sup>12</sup>. Pseudo-communities were built

65 from pseudo-species adapted to temperature fluctuations in a given region. We therefore focused on  
66 climate-induced changes that originate from fluctuations in the thermal regime and not from shifts  
67 induced by other environmental parameters<sup>19</sup> (e.g. nutrients, salinity, oxygen) or anthropogenic  
68 pressures (e.g. fishing, eutrophication and pollution)<sup>2</sup>. It is now a key principle in ecology that thermal  
69 tolerance is species-specific<sup>3</sup> and the strong influence of temperature on species through their thermal  
70 niche has been observed for a variety of ecosystems and taxonomic groups<sup>17,20,21</sup>. The novelty in this  
71 present analysis is our conceptual incorporation of the niche into a model that allows us to explore the  
72 influence of temperature at the community level in the context of climate-induced changes, including  
73 ACSs.

74

75 We first tested if our model's predictions of long-term changes in pseudo-communities agreed with  
76 independent observations from 14 multi-decadal series (Supplementary Figure 1; Supplementary  
77 Tables 2-3). These records included measurements of zooplankton (11 ecosystems), decapods (1  
78 ecosystem), and/or fish (4 ecosystems) spanning tropical (Hawaii) to polar regions (Southern Ocean),  
79 coastal (e.g. Adriatic and San Francisco Bay) to deep/open oceans (Pacific, Atlantic and Southern  
80 Oceans) and seas (Adriatic, Ligurian, North and Baltic Seas). For each observed community we  
81 performed a standardised Principal Components Analysis (PCA) on a matrix of years by biological  
82 variables (e.g. species abundance, biomass, or size fraction) and retained the first two Principal  
83 Components to investigate their long-term changes (Obs-PC1-PC2s). In each system, 10,000 PCAs were  
84 also performed on 10,000 pseudo-communities, each resulting from different simulated pseudo-  
85 species associations. From these, we retained 10,000 pairs of predicted changes (Pred-PC1-PC2s)<sup>12</sup>.  
86 We provide an illustrative case-example of the skill of our model for the North Sea (Figure 1). Here, the  
87 first obs-PC shows a pronounced change at the end of the 1980s for 43% of taxa, and our simulated  
88 first PC also exhibits the same pattern for 71% of the pseudo-species; both PCs were highly correlated  
89 (Figure 1a-b,e-f;  $r=0.83, p=0.01, n=50$ ).

90

91 When all 14 ecoregions are considered (Fig. 2a-n), 89% (25) of all first two observed eigenvalues are  
92 significant (Supplementary Table 4). The observed and predicted community changes are highly  
93 correlated for every ecoregion, except for the highly dynamic and heterogeneous<sup>22</sup> Western Pacific  
94 Transition Zone where only the two late-1980s and -1990s substantial shifts were predicted (Figure 2;  
95 Supplementary Note 1 and Table 5). Note that long-term changes shown in the figure are the examples  
96 showing the highest correlations between an observed and a predicted PC. As it might be expected,  
97 some observed PCs were weakly correlated with predicted PCs (Supplementary Table 5), which could  
98 be because i) some species may not react to temperature when their thermal optimum coincides with  
99 the mean local thermal regime<sup>12,23</sup>, or ii) some species may be more sensitive to other forcing (e.g.

100 anthropogenic pressure, other ecological factors, biotic interactions or local complex circulation  
101 patterns)<sup>5,19,22,24</sup>. Such differences in response may explain why the climatic signal identified by the  
102 PCAs was sometimes associated with PC1 and at other times with PC2. Therefore, to consider the full  
103 complexity of the signal, we used the first 2 predicted PCs (mean Pred-PC1-2, averaged over 10,000  
104 simulated PCs; Figure 2a-n) and applied a regression (Methods) that explained 50.4%  
105 ( $r=0.71, p<0.01, n=567$ , Fig. 2o) of the total variance of all observed long-term changes in the 14  
106 ecoregions (red Obs-PCs; Figure 2a-n). Since predicted communities are independent of the observed  
107 communities, correlations of observed and predicted PCs are higher than we expected. This suggests  
108 that our framework captures the main drivers of changing communities.

109

110 To verify that these results were not due to chance, we also examined correlations between  
111 observations and null models generated for each system and composed of random time series both  
112 with and without autocorrelation (Methods). Simulated Pred-PC1-PC2s from these null models  
113 exhibited a pronounced variability in each system, far exceeding that originating from METAL  
114 (Supplementary Figure 2 *versus* Figure 2a-n). All mean correlations were smaller than those expected  
115 from METAL, with the exception of the HOT time series. When all PCs were combined together (Fig.  
116 2o-p), the correlations based on METAL were substantially higher than could be explained by chance  
117 (Figure 2p). The small range in METAL/observation correlations (Fig. 2p, red bar) in comparison to null  
118 models (Fig. 2p, green and blue) indicates that results are stable, regardless of the selected pseudo-  
119 species. This suggests that inclusion of all species might not be necessary to assess a community's  
120 state. This is fortuitous because most monitoring programmes sample only a small part of a community  
121 (Supplementary Table 3).

122

123 Next, we tested the capability of our framework to reveal large-scale community changes, including  
124 ACSs, by combining results from all 14 ecoregions (Figure 3). To extract the overall biological variability,  
125 we performed 'global' PCAs on the first two Pred-PCs extracted from (i) simulated (METAL and the null  
126 model based on autocorrelated time series) and (ii) observed communities for the 14 systems (14  
127 systems x 2 PCs =28 variables for each PCA). Therefore, we used all of the first two observed and  
128 predicted PCs for this analysis, which represents the full set of interactions within the observed and  
129 predicted PCs (Supplementary Table 6). We chose the period 1960-2007 because it had less than 50%  
130 missing data per year in each time series (Supplementary Figure 3). We performed this procedure in  
131 two ways: (i) a single 'global' PCA based on the average of 10,000 PC1-PC2s for each system to calculate  
132 the correlation between observations and predictions from METAL, and (ii) 10,000 'global' PCAs to  
133 compare the variability of long-term changes from METAL and the null model. The first global PC  
134 originating from observed communities was highly correlated ( $r=0.87$ ) with the first global PC derived

135 from the mean of 10,000 theoretical communities (Figure 3a). Predicted and observed PC2s and PC3s  
136 were also significantly correlated, although at a lower level (Figure 3b-c). METAL predictions had  
137 smaller variability than predictions based on the null model (Figure 3a-c, green *versus* blue curves).

138

139 We verified the representativity of these time series with respect to the global ocean. While our 14  
140 initial sites or ecoregions span a range of water depths from 31 to 5492m, many are close to the  
141 coastline and so our results could be biased towards shallow marine environments (Supplementary  
142 Table 3). To address this possibility, we analysed observations in 5 additional regions of the North  
143 Atlantic where we had spatially and temporally consistent data from nearshore and offshore and from  
144 shallow to deep waters (Supplementary Note 1). This analysis confirmed the validity of our framework  
145 in open oceanic domains (Supplementary Note 1) even if no data were available to us from the centre  
146 of oceanic basins nor from the South Pacific, South Atlantic or Indian Oceans (Supplementary Note 1).

147

148 We then tested METAL predictions of abrupt shifts. Using pooled data from the 14 initial sites, we  
149 identified ACSs using an Abrupt Shift Detection (ASD) algorithm on 10,000 global PC1-PC3s (Methods).  
150 The algorithm detected a significant shift *circa* 1987 in our North Sea example for both predicted and  
151 observed first PCs (Figure 1c-d). For global PCs, the first two observed and predicted PCs showed  
152 significant ACSs at the end of the 1980s and 1990s respectively (Figure 3d-e). Predicted ACSs (blue  
153 curves) occurred one year before observed ACSs (red curves), possibly reflecting inertia related to  
154 species' life cycles<sup>16</sup>. This analysis shows that the most frequent (but not necessarily the most intense)  
155 shift in the ecoregions coincided with the well-documented events of the late 1980s (Figure 3a,d)<sup>4,6,7</sup>.  
156 Although they were not significant, we detected acceleration phases on both third predicted and  
157 observed PCs (Figure 3c,f). The well documented 1976/77 ACS<sup>15</sup> was not significant when all systems  
158 were considered (Fig. 3), probably because our observations did not include many areas where this  
159 shift occurred (Figure 2k, Supplementary Note 1). No significant trends were observed in global PCs  
160 based on autocorrelated time series (Figure 3d-f, green curves). These results suggest that our model  
161 can predict a substantial part of long-term community change, including ACSs.

162

163 We then used our ASD algorithm to predict ACSs in space and time by applying it to the whole ocean  
164 for the period 1960-2015 and covering areas and years not monitored. For this analysis, we did not use  
165 any PCA but applied our algorithm to pseudo-species and retained only ACSs when they involved half  
166 or more pseudo-species for a given location and year. Our analysis suggests that ACSs may occur every  
167 year, but only in a limited part of the ocean (~2.8%), involving on average an area of ~10 million km<sup>2</sup>  
168 of ocean per year (Figure 4a and Supplementary Figure 4). Some periods had geographically limited  
169 ACSs (e.g. 0.89 million km<sup>2</sup> for 1984-1987) whereas others showed more extensive shifts (e.g. 50.5

170 million km<sup>2</sup> for 2012-2015). Widespread predicted ACSs were always observed after El Niño events  
171 (e.g. weak El Niño episode of 1977-1978 and very strong episodes of 1997-1998 and 2015-2016) but  
172 not all El Niño events led to widespread ACS predictions (e.g. very strong episodes of 1982-1983; Figure  
173 4a). The late-1980s ACS, so frequently found in areas where monitoring took place<sup>4-6,8,11,12</sup>, was not  
174 predicted on a global scale. Despite similar strength in the two strong El Niño events 1997-1998 and  
175 2015-2016, the spatial extent of the predicted ACSs was very different, the recent one being more  
176 widespread (50 million km<sup>2</sup> *circa* 2014 *versus* 29 million km<sup>2</sup> *circa* 1999). The mean magnitude of ACSs  
177 increased substantially after the mid-2000s with a peak *circa* 2012 (Figure 4b). When both spatial  
178 extent (number of geographical cells) and magnitude were combined, an unprecedented shift (5 and  
179 3 times the average extent and magnitude, respectively) occurred after 2010 with a maximum ~2014  
180 (Figure 4c). Our null model (Figure 3d-f) showed that such an ACS at the end of the time series is  
181 unlikely to be an artifact as is sometimes reported with other techniques<sup>4</sup> (Methods).

182

183 The next question was whether the predicted ACSs could be associated to climate. We investigated  
184 these relationships using six climate parameters measured at a global scale: annual Sea Level Pressure  
185 (SLP), meridional and zonal winds, wind intensity, cloudiness, and Sea Surface Temperature (SST)  
186 (Methods). Using maps of ACSs and climatic shifts calculated for each year (Supplementary Figures 4-  
187 5), we found significant correlations (Supplementary Table 7) between the spatial extent of both  
188 predicted and observed ACSs from 1960 to 2015 with annual SLP ( $r=0.69, p_{ACF}<0.01, n=53$ ), atmospheric  
189 circulation (wind intensity and direction) variables ( $r=0.54-0.57, p_{ACF}<0.01, n=53$ ) and, as expected, with  
190 annual SST ( $r=0.97, p_{ACF}<0.01, n=53$ ). No significant correlation was found with cloudiness. These results  
191 identify a strong link between the spatial extent of predicted ACSs and shifts in atmospheric circulation  
192 and SST.

193

194 We subsequently calculated predicted shifts on a global scale, focusing on 5 time periods: 1975-1979,  
195 1985-1989 and 1995-1999 because these include previously documented ACS<sup>4-8,11,15</sup>, 2005-2009 as an  
196 example of a relatively stable period; and 2010-2014 because of its exceptional nature (Figure 5). The  
197 predicted 2014-2015 ACS, clearly evident by visual inspection (Supplementary Figure 4), is much more  
198 intense and widespread than previous shifts (Figures 4-5), encompassing meteo-oceanic warm  
199 anomalies in the Northwest Atlantic, Northeast Pacific Ocean and many areas of the Arctic Ocean and  
200 the central North-Atlantic cold blob<sup>9,25-27</sup>(Figure 5). Although changes in the North Atlantic and Pacific  
201 Oceans resulted in part from changes in atmospheric and oceanic circulation and its influence on  
202 regional thermal regimes, changes in the Arctic resulted mainly from abrupt shifts in annual SST (Figure  
203 5e,j, Supplementary Figure 6).

204

205 Our framework provides a theoretical explanation for long-term biological changes and ACSs. Each  
206 species responds individually, depending upon the interaction between its thermal niche and  
207 fluctuations in the thermal environment<sup>12</sup>, with cumulative responses leading to ecosystem shifts. The  
208 close correspondence between shifts in predicted and observed communities supports our framework  
209 and provides a useful basis for predicting climate/temperature-induced ACS at the community scale.  
210 However, large unexpected events such as the collapse or explosive growth of some populations  
211 (black-swan events<sup>28</sup>) may not be predicted by our approach.

212

213 Our ability to resolve the spatial extent of oceanic community shifts is severely constrained by a paucity  
214 and unrepresentative coverage of observations. Most marine communities, in particular marine  
215 metazoans, are hidden from earth observation tools and adequate monitoring coverage for the entire  
216 ocean is logistically unlikely. Our framework could therefore be meshed with existing monitoring  
217 programmes to provide a macroscopic tool for identifying regions likely to develop ACSs and to help  
218 anticipate biological perturbations that could affect production of ecosystem goods and services<sup>27</sup>. For  
219 example, our framework has predicted an ACS of unprecedented scale in 2014-2015 that may have  
220 substantial ecological consequences<sup>25,27</sup> across the Northern Hemisphere, including in the Arctic where  
221 current changes such as sea-ice melting are accelerating<sup>9</sup>. Finally, our study alerts us to the potential  
222 for a growing size and consequence of future ACS events as the world warms in response to rapidly  
223 increasing concentrations of atmospheric greenhouse gases. Even though it will remain difficult to  
224 predict ACSs, both because of model uncertainties and the fact that some event types will remain  
225 unpredictable<sup>29,30</sup>, the ability to forecast putative ACS events is an important development in our  
226 understanding of climate change biology.

227

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238

239

240 **Author contributions**

241 G.B. conceived the study; G.B., A.C., A.A., E.G., J.C., S.C. and all co-authors compiled the data and G.B.  
242 analysed the data. G.B. wrote the (initial draft) paper. G.B., A.C., A.A., P.C.R., E.G., J.C., R.R.K., S.O., S.C.,  
243 M.E. and all other co-authors discussed the results and contributed to the paper writing.

244

245 **Additional information**

246 The authors declare no competing financial interests. Supplementary information  
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251

252 **Data availability**

253 The authors declare that data supporting the findings of this study are available from the  
254 corresponding author upon request.

255

256 **Literature cited**

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328

## 329 **Figure legends**

330 **Figure 1 | Long-term biological changes and abrupt community shifts (ACSs) for both the observed**  
331 **community and a simulated pseudo-community in the North Sea. a-b.** Long-term changes of the first  
332 principal components (PCs) and in biological variables related to them (i.e. absolute values of the  
333 normalized eigenvector  $\geq 0.6$ ; blue): (a) observed species and (b) simulated pseudo-species. The first  
334 PC, reflecting major changes in community structure, is in black for observed taxa (a,e) and red (b,e)  
335 for simulated pseudo-species. Taxa related to the observed first PC included *Calanus finmarchicus*  
336 (negative relationship, -), *C. helgolandicus* (positive relationship, +), *Candacia armata* (+), *Centropages*  
337 *typicus* (+), *Corycaeus* spp. (+), and *Oithona* spp. (-). Ten pseudo-species were related to the simulated  
338 first PC. The grey band shows the timing of the ACS revealed in panels c-d. c-d. Detection of ACSs for  
339 the first PC based on (c) the observed community and (d) the simulated pseudo-community. The  
340 dashed red horizontal line indicates the threshold of 3 used throughout this study. e-f. Measured  
341 (black) and simulated (red) first PCs (e) and their relationships (f). This ecosystem, and most biological

342 systems considered in this study (except HOT, Southern Ocean and San Francisco Bay; see Methods)  
343 were also analysed in detail by Beaugrand<sup>12</sup> and Beaugrand and colleagues<sup>7</sup>, respectively.

344 **Figure 2 | Predicted (grey) and observed (red) long-term community changes for 14 systems.**

345 Principal components were standardised between -1 and 1. Pred-PC: 10,000 Principal Components  
346 (grey) based on 10,000 simulated communities. Obs-PC: Principal Component based on observed  
347 communities (red). **a.** North Sea (Pred-PC1s and Obs-PC1), **b.** Baltic Sea (Pred-PC1s and Obs-PC1), **c.**  
348 Adriatic Sea (Pred-PC1s and Obs-PC1), **d.** Ligurian Sea (Pred-PC2s and Obs-PC1), **e.** Northwest Atlantic,  
349 southern area (Pred-PC1s and Obs-PC2), **f.** Northwest Atlantic, northern area (Pred-PC1s and Obs-PC1),  
350 **g.** West Pacific Transition zone (Pred-PC1s and Obs-PC1), **h.** Oyashio (Pred-PC1s and Obs-PC1), **i.**  
351 CALCOFI (Pred-PC1s and Obs-PC1), **j.** San Francisco Bay (Pred-PC1s and Obs-PC1), **k.** East Pacific region  
352 (Pred-PC1s and Obs-PC1), **l.** West Pacific region (Pred-PC1s and Obs-PC2), **m.** HOT (Pred-PC1s and Obs-  
353 PC2), **n.** Antarctic Peninsula area (Pred-PC1s and Obs-PC2). **a-n.**  $r_m$  are the mean linear correlations  
354 between the mean of 10,000 predicted and the observed community PC. Biological variables  
355 considered at each site are indicated by **D** (benthic decapods), **Z** (zooplankton), and **F** (Fish). Biological  
356 variables are indicated in the Methods.  $x|y$ :  $x$  is the number of pseudo-species used in METAL and  $y$  is  
357 the number of time periods (1 indicates the annual value). The total number of variables used in  
358 METAL model is the product of  $x$  and  $y$ . For California Current (total zooplankton biomass) and Hawaii  
359 (zooplankton size fractions), we chose arbitrarily pseudo-communities composed of 30 pseudo-  
360 species. **o.** Long-term community shifts predicted from a regression on principal components, using  
361 the first two Pred-PCs from the 14 systems (averaged from the 10,000 first 2 PCs) and observed  
362 community shifts as in panels **a-n**. **p.** Histograms of the 10,000 correlations between selected Obs-PCs  
363 and predictions based on the first 2 Pred-PCs from (i) the null model based on random time series  
364 (grey), (ii) randomly generated time series with an order-1 autocorrelation  $\geq 0.5$  (blue), and (iii) the  
365 METAL theory (red).

366

367 **Figure 3 | Comparisons of observed (red) and predicted (blue and green; 10,000 simulations)**

368 **community shifts, all ecoregions combined.** Model predictions are in blue and predictions from a null  
369 model with autocorrelation in green. **(a)** First PC (30.72% of the total variance): predicted and observed  
370 community changes. **(b)** Second PC (21.46%): predicted and measured community changes. **(c)** Third  
371 PC (15.47%): predicted and observed community changes. Index of abruptness of predicted and  
372 observed community changes: **(d)** First PC. **(e)** Second PC. **(f)** Third PC. Correlation ( $r$ ), probability of  
373 significance without ( $p$ ) and with ( $p_{ACF}$ ) correction for temporal autocorrelation, and degree of freedom  
374 ( $n$ ) are indicated in panels **a**, **b** and **c** and correspond to the correlation calculated between  
375 observations and METAL predictions when all local PCs are averaged. In **d-f**, the wide blue (METAL)

376 and green (null model) curves correspond to the medians of 10,000 simulations and the lower and  
377 upper part, are the 5<sup>th</sup> and 95<sup>th</sup> percentiles, respectively. The first three axes of the PCA performed on  
378 observed data were significant using a statistical test based on a broken-stick distribution (Methods).

379

380 **Figure 4 | Predicted long-term variation of Abrupt Community Shifts (ACSs) in the global ocean. (a)**  
381 **spatial extent, (b) magnitude and (c) spatial extent and magnitude of ACS.** Curves in red are order-1  
382 moving average of predicted values (blue bars) (Methods). Thin-dashed, thin-solid and thick red arrows  
383 identify weak, moderate, and strong El Niño events, 'E' = super El-Niño events. Thin and thick blue  
384 arrows identify moderate and strong La Niña events.

385

386 **Figure 5 | Predicted Abrupt Community Shifts (ACSs; a-e) and climatic shifts (f-j) during the period**  
387 **1960-2015 with a focus on the years 1975-1979 (a and f), 1985-1989 (b and g), 1995-1999 (c and h),**  
388 **2005-2009 (d and i) and 2010-2014 (e and j).** Colour bars show the percentage of individual time series  
389 having a significant shift (threshold>3). For ACSs, 50% means that half the pseudo-species exhibited a  
390 significant shift for a given pseudo-community. For climatic shifts, 50% means that half the climate  
391 parameters (3 of 6 parameters) had a significant shift. White areas are regions with no shift. When the  
392 percentage of shifts is >0, the percentage is indicated by a colour: yellow and red for low and high  
393 percentage, respectively. The six climatic parameters are: annual Sea Level Pressure (SLP), meridional  
394 wind, zonal wind, wind intensity, cloudiness and annual sea surface temperature (SST). The spatial  
395 extent of ACSs increases when the climatic shifts are more widespread. Individual maps of all predicted  
396 ACSs and observed climatic shifts are displayed in Supplementary Figures 4-5. Black arrow: direction  
397 and intensity of mean annual wind (1960-2015). Black line: isobar based on mean annual SLP (1960-  
398 2015).

399

## Methods section

### Materials

#### Sea surface Temperature

Annual SSTs originated from the dataset ERSST\_v3 (1960-2015). The dataset is derived from a reanalysis based on the most recently available International Comprehensive Ocean-Atmosphere Data Set (ICOADS). Improved statistical methods have been applied to produce a stable monthly reconstruction, on a 2° x 2° spatial grid, based on sparse data<sup>31</sup>. Data were interpolated on a global grid of 1° latitude x 1° longitude.

#### Sea Level Pressure, wind and cloudiness

Sea Level Pressure (SLP), cloudiness and both the meridional (V) and the zonal (U) components of the wind were extracted from the National Center for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) Reanalysis project<sup>32</sup>. NCEP uses a climate model that is initialised with observations originating from a variety of sources (e.g. ships, planes and satellite observations). The spatial grid (2.5° latitude x 2.5° longitude) of annual average SLP and U and V wind data were constructed for the period 1960-2015. Wind intensity was calculated from U and V wind. Data were interpolated on a global grid of 1° latitude x 1° longitude for the period 1960-2015.

#### Observed biological data

We used a summary of long-term community shifts (i.e. the first 2 principal components after applying a Principal Components Analysis, PCA) in 14 regions located in three oceans (the Atlantic, the Pacific and the Southern Oceans) and four Longhurst biomes<sup>33</sup> (Polar, Westerlies, Trade-Winds, and Coastal biomes). The first 11 regions have been analysed by standardised PCA in Beaugrand and colleagues<sup>7</sup>, the 12<sup>th</sup> has been analysed in Cloern and colleagues using the same technique<sup>34</sup> and both the 13<sup>th</sup> and 14<sup>th</sup> time series were added to the present study, following the same procedure. Supplementary Note 2 summarized the main characteristics of the 14 selected regions (see also Supplementary Figure 1 and Supplementary Table 2 for more details).

## Models and numerical procedures

438

439

### 440 Overview of the METAL theory

441

442 We applied a framework based on the MacroEcological Theory on the Arrangement of Life  
443 (METAL)<sup>12,16-18,35,36</sup>, a theory that explains how marine pelagic metazoans are arranged in the  
444 sea and how changing environmental conditions alter biological arrangements in space and  
445 time at different organisational levels (e.g. species, community, ecosystem), allowing precise  
446 predictions to be tested. METAL proposes that biodiversity is to a large extent influenced by  
447 climate and the environment. This influence mainly takes place through the interactions  
448 between the species ecological niche (*sensu* Hutchinson<sup>37</sup>) and both climatic and  
449 environmental changes. This interaction determines in large part the arrangement of life in  
450 the oceans at different organisational levels from the species to the ecosystem level and from  
451 small to large ecosystems<sup>18</sup>. More information on the METAL theory is available in  
452 Supplementary Note 3.

453

### 454 Generation of pseudo-species and pseudo-communities

455

456 To construct long-term changes in pseudo-community in each geographical cell of the global  
457 ocean, we used here the model described in Beaugrand<sup>12</sup> and Beaugrand and colleagues<sup>17</sup>;  
458 this model only uses one environmental parameter: temperature. We create pseudo-species,  
459 each having a unique Gaussian thermal niche with distinct degrees of eurythermy and  
460 thermophily<sup>16,17,38</sup> (Supplementary Figure 7, step 1). The response curve of the abundance  $E$   
461 of a pseudo-species  $s$  in a given site  $i$  and time  $j$  to change in SSTs was modelled by the  
462 following function<sup>17,39</sup>:

463

$$464 \quad E_{i,j,s} = c_s e^{-\left(\frac{(x_{i,j} - u_s)^2}{2t_s^2}\right)} \quad (1)$$

465

466 With  $E_{i,j,s}$  the expected abundance of a pseudo-species  $s$  at location  $i$  and time  $j$ ;  $c_s$  the  
467 maximum value of abundance for species  $s$  fixed to one;  $x_{i,j}$  the value of SST at location  $i$  and  
468 time  $j$ ;  $u_s$  the thermal optimum and  $t_s$  the thermal amplitude for species  $s$ . The thermal  
469 tolerance is an estimation of the breadth (or thermal amplitude) of the species thermal  
470 niche<sup>39</sup>.

471

472 A large number of pseudo-species was created with  $u_s$  varying between  $-1.8^\circ\text{C}$  and  $40^\circ\text{C}$  by  
473  $0.1^\circ\text{C}$  increments and  $t_s$  varying between  $1.1^\circ\text{C}$  and  $10^\circ\text{C}$  by increments of  $0.05^\circ\text{C}$ . This  
474 represented a total of 39,218 potential species. However, to consider niche vacancy<sup>38</sup>, we  
475 randomly selected half of this number<sup>17</sup>. At the end of the procedure, the global pool of  
476 pseudo-species was equal to 19,609; pseudo-species were randomly chosen to create local  
477 pseudo-communities (Supplementary Figure 7, step 1) so long as they could withstand the  
478 local temperature (annual SST) regime (Supplementary Figure 7, steps 1-3).

479

480 In each geographical cell, a pseudo-community was composed of a given number of pseudo-  
 481 species (see the map in Supplementary Figure 7). A similar biodiversity map generated by the  
 482 procedure can also be seen in Beaugrand and colleagues (their figure 1a)<sup>17</sup>. Each pseudo-  
 483 species has an index of abundance varying between 0 and 1 (Supplementary Figure 7, step 4).  
 484 The expected abundance of such pseudo-species was determined by linear interpolation from  
 485 the pseudo-species' thermal niche and monthly SSTs in a given geographical cell from 1960 to  
 486 2015 (Supplementary Figure 7, step 4). The procedure has been evaluated in detail for the  
 487 North Sea by Beaugrand<sup>12</sup>.

488  
 489 A summary of the state of the community is subsequently made by Principal Components  
 490 Analysis (PCA), using the first two principal components (Supplementary Figure 7, step 5).  
 491 More details on this analysis are presented in subsequent sections.

### 492 493 **Detection of Abrupt Community Shifts**

494  
 495 Many methods have been proposed<sup>40,41</sup>. Shift detection can be accomplished by the use of  
 496 the coefficient of variation<sup>41</sup>, the measure of the autocorrelation<sup>42</sup>, or the quantification of  
 497 the multi-scale variance along time series<sup>43</sup>. Here, we calculated an index of abruptness to  
 498 identify in a simple way Abrupt Community Shifts (ACSs). Our abrupt shift detection algorithm  
 499 was a simplified version of the methodology developed in Beaugrand and colleagues<sup>43</sup>. This  
 500 index was developed because (i) it does not require stable states in contrast to other  
 501 algorithms, (ii) it identifies a shift by evaluating the variability of the time series and (iii) it can  
 502 be applied in the intensive research of ACSs on a global scale. For a given time series, we first  
 503 calculated the order-1-5 difference of a time series where observations were standardised  
 504 between 0 and 1. Be  $\mathbf{Z}$  a time series,  $\mathbf{Z}=[z_i]$  was standardised as follows:

$$505$$

$$506 \quad x_i = \frac{z_i - \min(z)}{\max(z) - \min(z)} \quad (2)$$

507  
 508 The amplitude vector  $\mathbf{A}^p=[a_i^p]$  was subsequently calculated as the first p difference between a  
 509 value of  $\mathbf{X}=[x_i]$  at year t+p and year t, with  $1 \leq p \leq 5$ :

$$510$$

$$511 \quad a^p = |x_{t+p} - x_t| \quad (3)$$

512  
 513 After transformation, the time series has a length of n-p. This transformation enables the time  
 514 series to become stationary (i.e. constant mean, variance and autocorrelation structure), an  
 515 important assumption for many statistical tests. The magnitude vector  $\mathbf{M}^p=[m_i^p]$  was  
 516 subsequently calculated by making the ratio of the amplitude of change a on the average  
 517 amplitude of the time series:

$$518$$

$$519 \quad m_i^p = \frac{a_i^p}{\frac{1}{n-p-1} \sum_{j=1, i \neq j}^{n-p} a_j^p} \quad (4)$$

520  
 521 The denominator can reach values up to 1; therefore, for a constant numerator, the smaller  
 522 the denominator the higher the values of  $\mathbf{M}$ . On 100 simulated time series of 10,001 points,

523 95% of the 10,000 first differences ranged between 2.29 and 2.37. To be conservative, we  
524 selected a detection threshold of 3. Any values above 3 were considered to be indicative of an  
525 abrupt shift. We also used an order-1 symmetrical moving average prior to the application of  
526 the abrupt shift detection algorithm to diminish the influence of white noise in biological time  
527 series. Test of the procedure can be found in Supplementary Note 4 (see also Supplementary  
528 Figures 8-13).

529

### 530 **Relationships between observed and predicted long-term community shifts**

531

532 To test whether the METAL model was able to reproduce well long-term community shifts  
533 (including Abrupt Community Shifts or ACSs), we compared METAL predictions of long-term  
534 pseudo-community shifts with observed community shifts in 14 oceanic regions  
535 (Supplementary Figure 14). We applied a standardised PCA on a table years x biological  
536 variables and used the first 2 principal components to characterise biological changes in each  
537 of the 14 regions for which we had data. For 12 of those regions, the standardised Principal  
538 Components Analyses (standardised PCAs) were already performed<sup>7</sup> and we applied a similar  
539 procedure for the two others: (i) HOT station and (ii) Antarctic Peninsula area. Note that the  
540 standardised PCA for San Francisco Bay was updated to 2013 using the same procedure<sup>34</sup>. We  
541 tested the significance of the first two axes (eigenvalues) by using a broken-stick distribution<sup>44</sup>  
542 (Supplementary Table 7).

543

544 We calculated long-term pseudo-community shifts in each of the 14 regions by applying the  
545 procedure described in Beaugrand<sup>12</sup>; we produced a pool of pseudo-species that were able to  
546 colonise each of the 14 regions so long as they could withstand annual changes in SSTs  
547 (Supplementary Figure 7; see the section “Generation of pseudo-species and pseudo-  
548 communities”). The generation of the pseudo-species was made using Equation (1) for the  
549 period 1960-2015. Many pseudo-species were produced. However, only pseudo-species with  
550 an annual relative (i.e. expressed as percentage) abundance > 0.005 and a presence > 6% for  
551 all years of the time period were kept<sup>45</sup>. As more pseudo-species were generated than  
552 observed biological variables involved in the calculations of the summary of each observed  
553 community shifts, we chose randomly, for each region, a number of pseudo-species that  
554 corresponded to the number of biological variables (Supplementary Table 3 and  
555 Supplementary Figure 14). For example in the Pacific Rim, we selected a number of pseudo-  
556 species that corresponded to the number of biological variables used to perform the PCA.  
557 However, when total zooplankton biomass (CalCOFI) or size fractions (HOT) were used, we  
558 arbitrarily chose 30 pseudo-species and also chose two 2-month periods instead of a single 4-  
559 month period for the Southern Ocean. For CalCOFI and HOT, the selection of this number of  
560 pseudo-species did not affect significantly the results above 5 pseudo-species. For the  
561 Southern Ocean, the selection of two 2-month periods instead of one 4-month period reduced  
562 the variability of the different trajectories but did not strongly affect our conclusions. We  
563 repeated the selection of the pseudo-species 10,000 times and recalculated each time the first  
564 two principal components on pseudo-species (Supplementary Figure 14). Therefore, 10,000  
565 PCAs were performed for each of the 14 regions. When the number of pseudo-species was  
566 high in a given system, variability in the METAL predictions was low.

567

568 We subsequently compared the first two observed and predicted Principal Components (PCs)  
569 of the 14 regions; Obs-PC for PCs from the PCA based on observed community and Pred-PC

570 for PCs from the PCAs based on pseudo-communities (PC1 and PC2 for first and second  
571 principal components, respectively). This comparison was made in 3 different ways  
572 (Supplementary Figure 14).

573

574 First, we calculated the linear correlation coefficients between each Obs-PC and the average  
575 of the 10000 Pred-PCs (Supplementary Table 4); when the average was calculated,  
576 probabilities were calculated with and without adjusting the degree of freedom to correct for  
577 temporal autocorrelation<sup>46</sup>. Based on the correlation coefficients, we represented the best  
578 relationships between one of the two Obs-PCs and Pred-PCs for the 14 systems (Figure 2).

579

580 Second, we performed a regression on Principal Components<sup>47</sup> between the Obs-PC selected  
581 in Figure 2a-n and the first two corresponding Pred-PCs (averaged for the 10000 simulations)  
582 for the 14 systems. Those analyses were performed because they better integrate the  
583 complexity of the temporal signal of predictive PCs and removes any bias related to the  
584 selection of a given Pred-PC. A scatterplot was then performed between observed and  
585 modelled Obs-PCs of all systems and a linear correlation coefficient was calculated (Figure 2o).  
586 We also repeated the procedure for every simulation (10000) to examine the variability of the  
587 correlations between observed and predicted PCs (Figure 2p, red bars).

588

589 Third, we calculated two 'global' standardised PCAs: the first, on the matrix that combined the  
590 first 2 Obs-PCs obtained from each PCA applied on observed communities; the second, on the  
591 matrix that resulted from the combination of the first 2 Pred-PCs obtained from PCAs applied  
592 on simulated pseudo-communities (after averaging the 10,000 simulations). Prior to these  
593 analyses, we estimated the number of missing data from 1950 to 2014 to select a time period  
594 for which years had less than 50% of missing data (period 1960-2007; Supplementary Figure  
595 3). This threshold of 50% was chosen to have a maximum of years in the analyses with an  
596 alteration towards the beginning and the end of the selected time period as low as possible.  
597 We examined the relationships between the first 3 global Obs-PCs and Pred-PCs. We tested  
598 the significance of the first three axes by using a broken-stick distribution<sup>44</sup>. Normalised  
599 eigenvectors (i.e. correlations between long-term changes in the value of each variable with  
600 the first three principal components) are in Supplementary Table 5. This analysis focused on  
601 the different long-term and more abrupt patterns that were observed in the 14 systems. We  
602 also repeated the procedure for every simulation (10000) to examine the variability of the first  
603 3 predicted global PCs (Figure 3a-c; curves in blue) and its influence on the detection of ACSs  
604 (Figure 3d-f; curves in blue). We applied our abrupt shift detection algorithm to identify ACSs  
605 in the three global Obs-PCs and Pred-PCs. For this analysis, we used an order-3 weighted  
606 difference in all analyses after having applied an order-1 symmetrical moving average (see  
607 Equation 4 with  $p=3$ ). This procedure was chosen to remove the effects of episodic events and  
608 to concentrate on ACSs that may have persistent effects.

609

## 610 **Null models**

611

612 We designed two null models to examine whether our METAL predictions fit better the  
613 observations than those obtained randomly (with and without temporal autocorrelation;  
614 Supplementary Figure 14). The first null model generated a number of random time series for  
615 each station corresponding to the species richness simulated by METAL, with a length  
616 corresponding to the time period covered in each sampling site (Figure 2) and a length

617 corresponding to the time period chosen to perform 'global' PCAs (Figure 3). The second null  
618 model generated the same number of time series but using random time series with an order-  
619 1 temporal autocorrelation  $\geq 0.5$  as many of our observed and METAL-simulated time series  
620 were autocorrelated. We analysed those data using the same procedures applied to analyse  
621 METAL-simulated data (see the previous section) and to examine the relationships with  
622 observed biological data (Supplementary Figure 14). We only represented expected biological  
623 changes based on the null model using randomly generated time series with an order-1  
624 autocorrelation  $\geq 0.5$  as the null model based on random time series gave similar results. The  
625 average correlation between expected and observed changes was reported for each site  
626 (Supplementary Figure 2).

627

628 Subsequently, we calculated regression on PCs (the first two PCs for each system) using the  
629 same procedure as above for every expected Pred-PCs (therefore 10000 times). We  
630 performed this analysis for both random time series and randomly generated time series with  
631 an autocorrelation  $\geq 0.5$ . A histogram of all correlations (random time series and randomly  
632 generated time series) was performed and compared with correlations based on the METAL  
633 model (Figure 2p). Green: correlations between Pred-PCs based on random time series and  
634 Obs-PCs; Blue: correlations between Pred-PCs based on randomly generated time series with  
635 an order-1 autocorrelation  $\geq 0.5$  and Obs-PCs; Red: correlations between Pred-PCs based on  
636 the METAL model and Obs-PCs.

637

638 We calculated 'global' PCAs based on the 10000 Pred-PCs originating from Pred-PCs based on  
639 randomly generated time series with an order-1 autocorrelation  $\geq 0.5$ ; 10000 global PCAs were  
640 thereby calculated to examine the variability of the first 3 'global' PCs (Figure 3a-c; green). We  
641 also applied the Abrupt Shift Detection algorithm on each global PC (1-3 global PCs) and  
642 represented the 5<sup>th</sup>, 50<sup>th</sup> (median) and 95<sup>th</sup> percentiles (Figure 3d-f; green).

643

#### 644 **Predictions of Abrupt Community Shifts**

645

646 After testing our theoretical framework and abrupt shift detection algorithm against field  
647 observations, we estimated theoretically ACSs from 1960 to 2015 in all areas of the oceans.  
648 Here also, only pseudo-species with an annual relative (i.e. expressed as percentage)  
649 abundance  $> 0.005$  and a presence  $>6\%$  for all years of the time period were kept<sup>45</sup>. In each  
650 geographical cell of the oceans, we estimated ACSs for all pseudo-species composing a  
651 pseudo-community. To estimate ACSs, we used an order-3 weighted difference after having  
652 applied an order-1 symmetrical moving average (see Equation 4 with  $p=3$ ), as above. Then, we  
653 represented for each tested time period from 1960-1963 (mean year 1961.5) to 2012-2015  
654 (mean year 2013.5) the amount of species that exhibit ACSs out of the pseudo-species  
655 composing the pseudo-community (Supplementary Figure 4). Data of mean sea level pressure  
656 and mean wind circulation were superimposed on maps for the corresponding time period.  
657 Because the number of maps was large (see Supplementary Figure 4 for all maps), we chose  
658 5 time periods: (i) 1975-1979, 1985-1989 and 1995-1999 because these include already  
659 documented ACSs<sup>4,7,8,15,48</sup>, (ii) 2005-2009 because it is an example of a relatively calm period  
660 and (iii) the last period 2010-2014 (Figure 5). To pool different mean year of shift (e.g. 1976.5  
661 as an average of period 1975-1978) within those time periods (e.g. 1975-1979), we calculated  
662 the highest percentage of pseudo-species' shift in each geographical cell (e.g. 1975.5, 1976.5,  
663 1977.5, 1978.5, 1979.5).

664

## 665 **Observations of abrupt climatic shifts**

666

667 We applied the same procedure to identify abrupt climatic shifts from 1960 to 2015. We also  
668 applied an order-3 weighted difference after having applied an order-1 symmetrical moving  
669 average (see Equation 4 with  $p=3$ ). The abrupt shift detection algorithm was performed on  
670 annual sea level pressure, meridional (U) and zonal (V) wind, wind intensity, cloudiness and  
671 SST. We then added the number of significant shifts observed in each geographical cell from  
672 1960-1963 to 2012-2015 (Supplementary Figure 5). To examine the potential relationships  
673 between predicted ACSs and climatic shifts, we applied the same procedure as above for the  
674 same time periods: 1975-1979, 1985-1989, 1995-1999, 2005-2009 and 2010-2014 (Figure 4d-  
675 f). Abrupt climatic shifts were mapped for the period 2010-2014 for each climatic variable  
676 (2010-2014) in an attempt to understand the exceptional nature of the time period identified  
677 by our theoretical framework (Supplementary Figure 6).

678

## 679 **Long-term changes in spatial extent and magnitude of abrupt shifts**

680

681 For each year, we estimated the spatial extent, the magnitude, and both combined, of ACSs  
682 (Figure 5).

683

## 684 **Estimation of spatial extent of ACSs**

685

686 For each geographical cell that had a percentage of pseudo-species that shifted significantly  
687 above 50% in a given pseudo-community, geographical distances in a geographical cell were  
688 calculated as follows<sup>49</sup>:

689

$$690 \quad d(i,j)=6377.221 \times h_{i,j} \quad (5)$$

691 With  $d_{i,j}$  being the geographical distance between point  $i$  and  $j$ , the constant the Earth radius  
692 and  $h_{i,j}$  computed as follows<sup>49</sup>:

$$693 \quad h_{i,j} = ar \cos \left( \sin \varphi_i \sin \varphi_j + \cos \varphi_i \cos \varphi_j \cos g \right) \quad (6)$$

694 With  $\varphi_i$  the latitude (in radians) at point  $i$ ,  $\varphi_j$  the latitude (in radians) at point  $j$  and  $g$  the  
695 difference in longitude between  $i$  and  $j$ . The area was subsequently calculated by multiplying  
696 the zonal and meridional distance of the cell. Finally, we added all areas to obtain the spatial  
697 extent concerned by ACSs (Figure 4a). The same type of calculation was applied for each  
698 climatic variable that shifted significantly. This procedure allowed us to calculate the  
699 correlation (and its probability of significance  $p_{ACF}$ ; ACF means autocorrelation function)  
700 between long-term changes in spatial extent of significant ACSs and the spatial extent of  
701 climatic shift (threshold of 3) for each variable taken individually (Supplementary Table 6).

702

## 703 **Estimation of the magnitude of ACSs**

704

705 We also estimated the magnitude of ACSs for each year of the time period (1960-2015) by  
706 averaging the index of abruptness for each geographical cell for which more than 50% of  
707 pseudo-species shifted significantly (threshold of 3; Figure 4b).

708

709 **Estimation of both magnitude and spatial extent**

710

711 The last index was calculated by summing the magnitude of all ACSs characterised by at least  
712 50% of pseudo-species' shifts inside a pseudo-community. This index takes into consideration  
713 both the magnitude of the shift and the number of geographical cells concerned by an ACS  
714 (Figure 4c).

715

716

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